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CONTENTS

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SUBTRIBAL CLASSIFICATION OF THE ASTEREAE (ASTERACEAE)

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ABSTRACT

A classification of the tribe Astereae apportions the ca. 3020 species in 189 genera among fourteen subtribes. Seven subtribes are first proposed here (**Brachycominae, Chrysopsidinae, Feliciinae, Lageniferinae, Machaerantherinae, Podocominae,** and **Symphyotrichinae**); seven are previously described (Asterinae, Baccharidinae, Bellidinae, Conyzinae, Grangeinae, Hinterhuberinae, and Solidagininae). Three major groups are mostly restricted to the Southern Hemisphere: the Baccharidinae, Hinterhuberinae, and "the grangeoid complex," a loosely associated group of seven subtribes. A few genera of these groups independently reached the Northern Hemisphere (e.g., *Erigeron*, *Ericameria*, and *Townsendia* in western North America, *Bellium* and *Bellis* in the Old World). The Asterinae is the only subtribe that is primarily Asian; *Boltonia* is regarded as the only genus of Asterinae autochthonous in North America, and one species group of *Aster* sensu stricto apparently has radiated secondarily in southeastern Africa. Evolutionary radiation primarily in North America produced the Solidagininae, Symphyotrichinae, Machaerantherinae, and Chrysopsidinae, although the first two have representatives in Asia; elements of each of these four subtribes have reached South America. The Symphyotrichinae and Solidagininae appear to be closely related, as do the Machaerantherinae and Chrysopsidinae, and all four of these probably are closest to the Asterinae.

KEY WORDS: Astereae, Asteraceae, subtribes, classification

The tribe Astereae is here estimated to comprise ca. 3020 species in at least 189 genera. Bentham (1873a) recognized seven morpho-geographical groups ("types") of Astereae, each named for a typical member: *Aster*, *Erigeron*, *Bellis*, *Grangea*, *Solidago*, *Conyza*, and *Baccharis*. To describe intergeneric

relationships within and among many of these, he used the phrases "passes into," "touches," and "blends with," noting that many of the genera "pass into each other through exceptional or intermediate forms" (p. 402). Indeed, there are few non-parallel or non-convergent features that can be consistently used to define the infra-tribal subgroups; the Astereae appears to be among the most morphologically conservative tribes in the family. The boundaries of Astereaean genera, however, are now more clearly delimited as a result of the concentrated taxonomic studies at the generic level in the past 20 years, and the description of patterns of intergeneric relationship has become more critical.

In spite of his reluctance to delimit formal groups, Bentham (1873b) arranged the genera of Astereae into six subtribes, combining his "*Erigeron* group" and "*Bellis* group" into one, and he was essentially followed in this by Hoffmann (1890). In a much later systematic review of the tribe, Grau (1977) noted both the apparent artificiality in the existing subtribal classification and the difficulty in arriving at a more natural one, and he presented an arrangement of genera based simply on geographic distribution. Velez (1981) recognized a number of informal groups of New World Astereae (mostly South American) based primarily on achene morphology, but there are many difficulties with his interpretations and his proposed groupings did not move far beyond what was already understood or presumed. Zhang & Bremer (1993 = Z&B) arranged most of the genera of Astereae into 23 informal groups (leaving 17 genera as "isolated") and scored one genus of each of the groups for 26 characters. A hypothesis of relationships within the tribe was derived from their cladistic analysis of these 23 taxa. Three subtribes were recognized by Z&B: the Asterinae, Grangeinae, and Solidagininae.

As a result of my own attempts to discover patterns of relationship within the Astereae, I have formulated hypotheses delimiting several generic groups: subtribe Solidagininae (Nesom 1993a), the goldenaster group (Nesom 1991b), subtribe Hinterhuberinae (Nesom 1993b, 1993c, 1993g), subtribe Baccharidinae (Nesom 1993b), and subtribes Asterinae and Symphyotrichinae (Nesom 1994k). Morgan & Simpson (1992) provided a phylogenetic overview of the *Machaeranthera* group, based on analysis of restriction site variation in chloroplast DNA; their delimitation of that group is modified only slightly in the present report. Nesom *et al.* (1990) presented a phylogenetic overview of the North American Astereae, based on an amalgamation of the molecular data of Suh (1989) and Morgan (1990). In the present study, I have attempted to proceed by developing a first-hand knowledge of species in problematic groups, which sometimes has necessitated redefinition of the genera involved. The subtribal concepts have been constructed by the accretion of related genera out to what appear to be the natural limits of the group. Remaining problems are pointed out in numerous instances as the discussion proceeds as well as in a separate section.

The broad view of Astereaean phylogeny and classification (and associated extrapolations and implications, especially regarding biogeography) presented by Z&B is widely divergent from that suggested by my studies. There is similarity between our delimitation of some of the generic groups (*i.e.*, in the terminology of Z&B, the *Amellus*, *Aster*, *Chiliotrichum*, *Chrysopsis*, *Grangea*, *Grindelia*, *Olearia*, *Solidago*, and *Vittadinia* groups, relying in significant degree on the same recently published studies), but there are wide differences in others (*e.g.*, their *Erigeron-Conyza* group comprises elements of seven subtribes in my view). In a retrospective view of the Z&B analysis, Bremer (1994, p. 382) has noted that "Zhang and Bremer did not claim to present a robust phylogenetic hypothesis for the Astereae. Rather, they attempted to demonstrate monophyletic or nonmonophyletic status for the subtribes in the light of existing morphological evidence." The results of the analysis presented here, however, based on the same "existing morphological evidence," differ so strongly from theirs that it suggests that even their test for broad patterns of infratribal monophyly may have been unsuccessful. Despite the avowal by Z&B of the necessity for a cladistic methodology in the delimitation of genera and higher taxa (also see Bremer & Humphries 1993, p. 74 - "Taxonomic Concepts"), the efficacy of their approach in the Astereae, versus the more traditional one followed here, will be evaluated only by further, independent studies.

The initial arrangement of genera into "groups" is the primary similarity in approach between the present study and that of Z&B. The scoring of character states by Z&B, however, further contributed to the disparity between their conclusions and mine, as it led to further associations of genera that are here considered widely separated in phylogenetic position. Their scoring of some characters appears to be simply incorrect, e.g., *Conyza* and *Erigeron* with angular or terete achenes (vs. flattened, 2-nerved), *Amellus* with (8-)10-ribbed achenes (vs. 2-5[-7]), *Corethrogyne* and *Grindelia* with style branch appendages longer than stigmatic areas (vs. shorter than stigmatic areas), *Grindelia* with style branch hairs slender, acute (vs. short, obtuse-rounded); their scoring of some characters of yet other taxa (representing generic groups) is highly equivocal in interpretation. Many of the characters are variable even within relatively small groups, and, in the approach of Z&B, the inter-relationships within each group represented in the analysis would necessarily have to be understood well enough that the most primitive member of each could be selected as its representative.

The choice of an outgroup had a significant influence on the topology of the cladistic relationships hypothesized by Z&B (as they themselves noted). Their analysis placed the Grangeinae as the sister group to the rest of the tribe, based on a single feature of leaf morphology (margins "pinnatifid-pinnatisect or at least distinctly serrate-dentate" vs. "entire or sparsely serrate-dentate only"). This interpretation was concomitant with their use of the subtribe

Anthemideae as the outgroup to the Astereae. The Astereae and Anthemideae also were placed as sister groups in the broad morphological survey and phylogenetic analysis recently completed by Karis (1993a). The Astereae has been variously positioned within the Asteroideae in other morphological and molecular studies, but the most recent ones have tended to place the Astereae and Anthemideae as sister groups (see Kim *et al.* 1992; Bremer *et al.* 1992), confirming a proximity of relationship that has been recognized since Cassini (1817) and Bentham (1873a).

Grau (1977) and Zhang & Bremer (1993) have furnished useful compilations of systematic literature related to the genera of Astereae. The overview by Bremer (1994) is essentially a recapitulation of the Z&B paper, but he has provided a short description for most of the genera. In the present paper, I have not attempted to include (with much duplication) all taxonomic references relating to the Astereae but rather those documenting the following discussion or augmenting the lists by Grau and Z&B. Supplemental references are provided in recently published studies of particular groups.

DEFINITION OF THE TRIBE ASTEREAE

Grau (1977) noted that the Astereae is particularly distinguished by four features. The discussion of these has been augmented and extended by Karis (1993a), who has furnished a useful, comparative characterization of the tribe.

(1) Style branches of the disc flowers have lateral stigmatic lines and lanceolate to deltate apical collecting appendages (sometimes referred to as "sterile appendages"). The inner surface of the branches and collecting appendages is glabrous (Jones 1976; Karis 1993a), with sweeping hairs (or collecting hairs) on the outer surface; the sweeping hairs range from short-papillate to longer with rounded apices, less commonly with pointed apices. In a survey primarily of North American Astereae, Jones (1976) observed that the disc style branches are pronate at maturity, rather than supinately spreading as in the rest of the family and as in the style branches of ray flowers in Astereae.

(2) Anthers have broadly lanceolate, eglandular apical appendages (glandular only in *Cyathocline*) and truncate to slightly auriculate bases. Anther bases are conspicuously "tailed" (caudate) in some genera of the Hinterhuberinae or slightly calcarate in species of a few genera (e.g., *Grindelia*).

(3) Pollen grains caveate with internal foramina, of the generalized type referred to as "helianthoid" (Skvarla *et al.* 1977).

(4) Achenes with a single-layered epidermis of cells thickened on three sides ("u"-cells) or less commonly all around. Subsequently, however, Grau (1980) found that such "u-cells" also occur in other tribes, considerably weakening

the diagnostic value of this character. Velez (1981) has provided a detailed investigation of achene morphology in American genera of Astereae.

Plants of Astereae are annual to perennial herbs to shrubs; small trees are found in the Baccharidinae and Hinterhuberinae; vines are rare and confined to the Baccharidinae and one species of Symphyotrichinae. Leaves are mostly alternate, opposite only within *Pteronia*, *Olearia*, and some African genera of subtribe Feliciinae.

Heads of Astereae are mostly heterogamous with tubular, 5-lobed, bisexual central flowers and ligulate, pistillate radial flowers. The tubular flowers often may be functionally staminate ("pseudo-hermaphroditic") with sterile ovaries, a phenomenon consistent within species and sometimes within genera, occurring independently in a number of subtribes; ray flowers rarely are sterile (e.g., *Corethrogyne*, *Galatella*, *Remya*). Dioecy has arisen independently in the Baccharidinae and the Hinterhuberinae (Nesom 1993b).

Ovarian sterility of disc flowers is sometimes a consistent character at the generic level within the Astereae; in the Podocominae, for example, it is characteristic of *Inulopsis* (4 species), *Minuria* (10 species), *Elachanthus* (2 species), and *Sommerfeltia* (2 species), as well as of the monotypic genera *Blakiella*, *Asteropsis*, and *Dimorphocoma*. Nevertheless, infra-generic variation in this feature is found in the Podocominae in Hawaiian *Tetramolopium* (Lowrey 1986) and *Ixiochlamys* (Dunlop 1980b) as well as in genera of other Astereaean subtribes, e.g., *Calotis* (Davis 1952); *Nidorella* (Wild 1969a); *Polyarrhena* (Grau 1970); *Zyrphelis* (Nesom 1994i); *Nolletia* (Hilliard & Burtt 1973); *Chrysopsis* (Nesom 1991a); *Ionactis* (Nesom & Leary 1992); *Chaetopappa* (Nesom 1992b); *Pacifigeron* (Nesom 1994j); and *Lagenifera* (Cabrera 1966).

The heads are commonly arranged in a corymboid capitulescence but this is sometimes modified to a secund or paniculate arrangement. For most of the primitively herbaceous generic groups of the Southern Hemisphere, heads are solitary or few in a loose capitulescence that could not be characterized as corymboid. Phyllaries are narrow, with an acute to rounded apex, often herbaceous, and usually in (2-)3-5 series that are graduated to nearly equal in length. Receptacles are generally epaleate; they are paleate in a number of genera of scattered phyletic affinity (e.g., *Achnophora*, *Geissolepis*, *Erodiophyllum*, *Ceruana*, *Amellus*, *Poecilolepis*, *Xanthisma*, *Callistephus*, *Eastwoodia*, and *Solidago*), where their occurrence cannot be taken as indication of close relationship (also see Ornduff & Bohm 1975 for notes on other genera with "marginal receptacular bracts"). In contrast, receptacular pales are more or less characteristic of generic groups in the Hinterhuberinae and Baccharidinae, where their evolutionary transmittal apparently has been more direct and indicative of common ancestry.

The disc corollas of Astereaean taxa may be abruptly ampliate, with a clearly differentiated limb sharply expanded above the tube and the staminal

filaments usually inserted at the tube-limb junction. In others, the corollas are narrowly tubular to narrowly funnelform, the limb not strongly differentiated from the tube. The lobes vary from short and erect or sharply recurved to long and recurved-coiling. Corollas are characteristically 4-lobed in some genera, especially in the Lageniferinae and Grangeinae. In a few, isolated genera, they are asymmetrical (e.g., *Heteropappus*, *Xylothamia*). These aspects of variation need to be investigated in more detail for their systematic implication, but a few examples of such variation are provided here: abruptly ampliate with short tube and short lobes (Grangeinae, Brachycominae, *Bellis*); abruptly ampliate with long lobes (*Baccharis*, *Solidago* and relatives, some primitive Symphyotrichinae); narrowly tubular with short, sharply reflexed lobes (Feliciinae, Podocominae); and funnelform with long, coiling lobes (some Hinterhuberinae). Druse crystals in the disc corolla tissues are common across the whole tribe; elongate prismatic crystals are conspicuous and characteristic of the limb and throat tissues of Chrysopsidinae (Nesom 1991b) and some Machaerantherinae (Nesom *et al.* 1993).

Pistillate (ray) flowers are in 1-several or numerous series, usually with a 3-5-veined ligule that may be acute to nearly truncate at the apex. The ligule sometimes is absent and the corolla then reduced to a short tube. In some Hinterhuberinae, the peripheral flowers are hypothesized to be derived from disc flowers (Nesom 1993b). Staminodia are present in the ray flowers of *Mairia*.

Ligules of ray flowers fall primarily into two color classes, yellow vs. white to bluish or pinkish. Most commonly they are white or some close variant, and considerable variation around this often occurs within a genus, but evolutionary transition to yellow rays has occurred independently in numerous, primitively and predominately white-rayed genera (white to yellow within *Brachycome*, *Calotis*, *Erigeron*, *Felicia*, *Hysterionica*, *Neja*, *Leptostelma*, *Zyrphelis*, *Pentachaeta*, *Psychrogeton*, *Townsendia*) or in generic lineages. There are completely yellow-rayed genera within otherwise essentially white-rayed subtribes: e.g., *Chrysocoma* (Feliciinae), *Nidorella* (Grangeinae), *Rochonia* (Hinterhuberinae). There are only three primitively yellow-rayed subtribes, the Chrysopsidinae, Solidagininae, and (probably) Machaerantherinae. Within these three subtribes, genera apparently have reverted to a white-rayed condition: e.g., *Noticastrum* (Chrysopsidinae), *Gundlachia* (Solidagininae), and *Xylorhiza* (Machaerantherinae); infrageneric reversions to white rays have occurred in species of the Solidagininae (e.g., within *Solidago*) and Machaerantherinae (*e.g.*, within *Machaeranthera*).

Achenes of Astereae are relatively small, mostly 1.5-3.0 mm long, but range considerably larger and slightly smaller; they commonly are flattened and 2-nerved, but in some groups they are multinerved and slightly angular or nearly terete in cross-section (*e.g.*, the Baccharidinae, Symphyotrichinae, variably in the Hinterhuberinae). Achene shape and nervation is generally constant within

a genus but rarely may be markedly variable (e.g., *Nardophyllum*, *Chaetopappa*, *Archibaccharis*). Achene surfaces commonly are glandular, especially in some Southern Hemisphere groups (also in the Asterinae), and usually produce duplex hairs (Zwillingshaare), these sometimes apically coiled or glochidiate. The pappus usually consists of barbellate bristles (plumose in *Zyrphelis*, *Gymnostephium*, some *Felicia*, *Monoptilon*, some *Vittadinia*, and *Mairia*); at least some taxa of all subtribes produce at least a few bristles, even in those with a strong tendency for pappus reduction or loss. There may be several series of pappus elements, the outer series or all sometimes reduced to scales, or the pappus may be reduced to only scales or even lost altogether. The pappus is usually persistent but may be basally caducous, a feature usually consistent within a genus or species group.

There are four commonly occurring types of trichomes in the Astereae:

(1) Type A (uniseriate, with thick cell walls, usually arising from a pedestal-like base);
(2) Type B (uniseriate, with thin cell walls, arising from a simple base);
(3) Type C (biseriate, with thin cell walls, usually glandular in function; these trichomes may simply consist of two rows of unmodified cells (common on the herbage of Conyzinae and Feliciinae and as achenial glands) or they may have a swollen head (consisting of the two terminal cells or a multicellular aggregation); the head may be sessile, sunken (punctate-glandularity), or stipitate, and in some groups it may produce a head of translucent, orangish resin (especially in the Asterinae, Chrysopsidinae, Machaerantherinae, Hinterhuberinae, and some Baccharidinae, these glands referred to by Grierson [1964] as the "glistening golden type"); and
(4) Zwillingshaare ("twin-hairs," Hess 1938: biseriate achenial hairs usually with thickened cell walls, with a basal mechanism for changing the orientation of the hair, and the terminal pair of cells with acute apices). The apex of the Zwillingshaare may be glochidiate (coiled or recurved, "anchor hairs") – see further comments below. This system of trichome nomenclature was adopted from a study of vestiture of "Inuloideae" by Drury & Watson (1966) and has been consistently used in the Astereae by Nesom (1976 and subsequent papers; especially see Nesom 1991b and reference to Semple *et al.* 1980). It was also recently adopted by Karis (1993a). Ramayya (1962) and Hellwig (1992) have offered detailed refinements and anatomical documentation of trichome types and a system of nomenclature from an ontogenetic perspective. These types of trichomes have been illustrated in various other publications (*e.g.*, Grierson 1964).

In glochidiate hairs, the apices of the distal pair of cells may be recurved in the same direction (coiled or hooked) or in opposite directions (glochidiate), the morphology usually constant within a species. The nature of such

modification has long been known and described (Gray 1880; Macloskie 1883), and a number of illustrations exist in relatively recent literature, *e.g.*, Rommel (1977), Turner (1984), and Elisens *et al.* (1992). Several variants of this type of Zwillingshaare are found in *Brachycome* and *Calotis*, the mound-like protuberances on achenes of these genera representing the most highly modified of these hairs (Davis 1952). Hairs with a glochidiate apex occur on achenes of at least some species of every genus of the Brachycominae, the consistent occurrence of this specialization interpreted here as an indication of common ancestry.

Within the Astereae, glochidiate Zwillingshaare are found outside of the Brachycominae in three species of *Minuria*, in *Amellus*, and in the Grangeinae. In the latter, they occur in the American *Egletes* and *Plagiocheilus*; in Old World Grangeinae, they occur in definite form in *Centipeda* and *Grangea* (see Fayed 1979), and the Zwillingshaare of *Grangeopsis* show a tendency for similar modification. As noted below, when other characters are considered, it seems likely that this similarity between the Grangeinae and Brachycominae may indicate closeness of common ancestry.

The base chromosome number in the Astereae is x=9, reduced to x=8, 7, 6, 5, 4, 3, and 2 (see summary and discussion of "Chromosome Evolution in the Astereae" in Nesom 1994k). Pentaynene, sesquiterpene lactones, benzofurans, and benzopyrans are absent. A few species of Astereae are cosmopolitan weeds, e.g., *Erigeron*, *Conyza*, *Solidago*, *Symphyotrichum*, and *Bellis*.

FORMAL DELIMITATION OF SUBTRIBES OF ASTEREAE

The formal, infratribal categories (14) delimited in the present study are more numerous than in previous classifications of Astereae. These groups, however, appear to be relatively clearly bounded. Phylogenetic interrelationships among the subtribes are more difficult to perceive within the Astereae on the basis of morphological evidence than are generic groupings themselves. Continuing studies within the Astereae based on comparative molecular data (several labs, in progress) may provide better resolved hypotheses of relationship as well as tests of the composition of major generic groups (subtribes, as defined here).

The Astereaean subtribes are treated below in alphabetical order for ease of reference. Informally named generic groups are delimited within most of the subtribes (*e.g.*, the "*Kalimeris* group" of the Asterinae, the "*Pentachaeta* group" of the Feliciinae); genera of some subtribes are sometimes separated geographically when morphological differences among them do not support obvious subgroupings. Morphological combinations exceptional to the definitions of the groups are found in some taxa of nearly all of these subtribes. Comments and discussions regarding the definitions of the subtribes and the

position and status of problematic genera and generic groups are in a separate section following the formal taxonomy. A complete list of Astereaean genera, with the taxonomic authority, number of species, and subtribal position for each, is provided in the Appendix. Where the number of species is indicated as "ca.," other figures based on this number must also be treated as approximate.

Astereae [Cass., J. Phys. Chim. Hist. Nat. Arts 88:195. 1819.].

1. Asterinae [Dumort., *Fl. Belg. Prodr.* 66. 1827.]. Type genus: *Aster* L.

Heterochrominae Benth. *in* Benth. & Hook. [*nom. invalid.*], *Gen. Pl.* 2:177. 1873. See comments regarding "Homochrominae Benth." under Solidagininae.

Herbs; leaves sessile-glandular or not, mostly entire, less commonly serrate; heads in a loosely corymboid capitulescence to solitary; phyllaries flat, mostly herbaceous; receptacles epaleate; ray flowers 1-seriate, with long, white to blue ligules (yellow in some *Psychrogeton*); disc flowers bisexual; disc style branches with short papillate collecting appendages; achenes obovate, flat, 2-nerved, often glandular, without glochidiate hairs; pappus (1-)2-(-3) seriate, of persistent bristles equal in length or with a short outer series. Base chromosome number, x=9. Species/genera, 306/14.

Aster group (x=9): *Aster*.

Galatella group (x=9): *Crinitaria* (x=9), *Galatella* (x=9), *Tripolium* (x=9).

Kalimeris group (x=9): *Boltonia* (x=9), *Callistephus* (x=9), *Heteropappus* (x=9), *Kalimeris* (x=9), *Miyamayomena* (x=9).

Asterothamnus group (x=9): *Asterothamnus*, *Kemulariella* (x=9), *Krylovia*, *Psychrogeton* (x=9).

Arctogeron group (x=9): *Arctogeron*.

Isolated (x=9): "para-Brachyactis" (x=9) (see comments in Nesom 1994k).

2. Baccharidinae Less., Linnaea 5:145. 1830. Type genus: *Baccharis* L.

   Heterothalaminae Endlicher, *Gen. Pl.* 5:372. 1837. Type genus: *Heterothalamus* Less.

   Trees, woody shrubs, or vines, rarely herbaceous or suffrutescent; leaves commonly punctate-glandular, entire to serrate; heads usually in a congested corymboid to paniculate capitulescence; phyllaries flat, mostly herbaceous; receptacles epaleate, paleate in some *Baccharis*, *Heterothalamus*, *Sarcanthemum*; pistillate flowers absent or 1-seriate, eligulate or with short, white ligules; disc flowers bisexual, ovaries sterile in New World genera and these dioecious; disc style branches with short, papillate collecting appendages; achenes small, terete, multi-nerved, usually eglandular (glandular in some *Baccharis* and *Archibaccharis*), without glochidiate hairs; pappus 1-seriate, of persistent bristles, often apically dilated. Base chromosome number, x=9. Species/genera, 479/11.

   Baccharis group: *Archibaccharis* (x=9), *Baccharis* (x=9), *Heterothalamus* (x=9).

   Psiadia group: *Heteroplexis*, *Microglossa* (x=9), *Psiadia* (x=9), *Psiadiella*, *Sarcanthemum*.

   Vernoniopsis group: *Vernoniopsis*.

   Commidendron group: *Commidendron*, *Melanodendron*.

3. Bellidinae Benth. *in* Benth. & Hook., *Gen. Pl.* 2:176. 1873. Type genus: *Bellis* L.

   Herbs; leaves in a basal rosette, eglandular, widely serrate-dentate; heads solitary on scapose stems; phyllaries flat, completely herbaceous, in 2(-3) series; receptacles sharply conical, epaleate; ray flowers 1-seriate, the ligules long, white or sometimes pink-tinged; disc flowers bisexual, fertile, the corollas with a short tube; disc style branches with deltate papillate collecting appendages; achenes obovate, flat, with a pair of thick, marginal ribs, eglandular, without glochidiate hairs; pappus absent or a short, laciniate crown, the insertion narrow. Base chromosome number, x=9. Species/genera, 8/1.

4. **Brachycominae** Nesom, *subtr. nov.*

Herbae; capitula pauca vel solitaria; phyllaria saepe marginibus latis hyalinis; receptacula conica; flores radii 1-seriati ligulis longis albis vel caeruleis; appendices collectentes breves papillatae ramorum styli florum disci; achenia obovata complanata 2-nervata, trichomata glochidiata ad superficies plerumque producta; pappus carens vel 1-seriatus setarum persistentium. Numerus basicus chromosomatum, x=9, ad 8,7,6,5, 4,3,2 deminutus. Typus subtribi: *Brachycome* Cass.

Herbs; leaves eglandular, entire or toothed to lobed; heads few or solitary; phyllaries flat, mostly herbaceous, often with broad, hyaline margins; receptacles epaleate (paleate in *Geissolepis*), conical; ray flowers 1-seriate (or multiseriate in some *Calotis*), with prominent, white to blue ligules, rarely yellow in *Townsendia*; disc flowers bisexual, with sterile ovaries in *Ceratogyne* and species of *Calotis*; disc corollas with a short tube below the abruptly expanded limb; disc style branches deltate or variously short with short, papillate collecting appendages; achenes obovate, 2-nerved, flat, 4-6 nerved and prismatic in *Aphanostephus* and *Geissolepis*, commonly winged in *Brachycome*, eglandular, the faces or margins usually with glochidiate hairs; pappus usually absent or highly reduced, less commonly 1-seriate, of persistent bristles. Base chromosome number, x=9, reduced to 8,7,6,5,4,3,2. Species/genera, 143/8.

a. [Australia]: *Brachycome* (x=9,8,7,6,5,4,3,2), *Calotis* (x=8,7,5,4), *Ceratogyne*.

b. [North America]: *Dichaetophora* (x=3), *Aphanostephus* (x=5,4,3), *Astranthium* (x= 5,4,3), *Geissolepis* (x=9), *Townsendia* (x=9).

5. **Chrysopsidinae** Nesom, *subtr. nov.*

Herbae glandulosae; capitula pauca vel solitaria; phyllaria saepe carinata zona apicali herbacea valde definita carenti; flores radii ligulis luteis; corollae disci crystallis grandis elongatis; appendices collectentes longi-lanceolatae patenti-pubescentes ramorum styli florum disci; achenia multinervata, strigosa; pappus persistens multiseriatus serie exteriore setarum vel squamarum. Numerus basicus chromosomatum, x=9, ad 7,6,5,4,3 deminutus. Typus subtribi: *Chrysopsis* (Nutt.) Elliott.

Herbs; leaves commonly stipitate-glandular, mostly entire; heads in a loosely paniculate capitulescence to solitary; phyllaries commonly keeled, herbaceous to chartaceous; receptacles epaleate; ray flowers 1-seriate, ligules long, yellow (or sometimes white in *Noticastrum*); disc flowers bisexual, corollas with large rectangular-prismatic crystals in the throat; disc style branches with long, hairy collecting appendages; achenes terete or angled, multinerved, usually eglandular, without glochidiate hairs; pappus 2-3(-4)-seriate, persistent, the inner of 1-2 series of generally flattened bristles, outer of much shorter setae, bristles, or scales. Base chromosome number, x=9, reduced to 7,6,5,4,3. Species/genera, 70/7.

Chrysopsis (x=5,4,3, secondarily x=9), *Croptilon* (x=7,6,5,4), *Heterotheca* (x=9), *Noticastrum* (x=9), *Osbertia* (x=5), *Pityopsis* (x=9), *Tomentaurum*.

6. Conyzinae Benth. *in* Benth. & Hook., *Gen. Pl.* 2:179. 1873. Type genus: *Conyza* L.

Herbs, sometimes stipitate-glandular, commonly coarsely pubescent, rarely woolly; leaves mostly entire, less commonly serrate, lobed or dissected in several groups of *Erigeron*; heads relatively few in a loosely corymboid capitulescence to solitary, densely paniculate in some *Conyza*; phyllaries flat, mostly herbaceous, with a prominent orange-glandular midvein (sometimes 3-veined); receptacles epaleate; pistillate flowers 1-seriate with white to bluish ligules, multiseriate in *Conyza* and *Erigeron*, with additional inner zone of eligulate pistillate flowers in *Erigeron* subg. *Trimorpha*; disc flowers bisexual; disc style branches with short, papillate collecting appendages; achenes obovate-oblong, flat, 2-nerved, eglandular, without glochidiate hairs; pappus 1-2(-3)-seriate, inner of persistent (rarely caducous) bristles, the outer series of short scales or setae (outer series mostly absent in *Conyza*), in the austrobrasilien genera the pappus sometimes of 2-3 series of nearly equal-length bristles. Base chromosome number, x=9. Species/genera, 513/6.

Conyza group: *Conyza* (x=9), *Erigeron* (x=9).

Leptostelma group: *Apopyros*, *Hysterionica* (x=9), *Leptostelma* (x=9), *Neja*.

7. **Feliciinae** Nesom, *subtr. nov.*

Herbae vel suffruticosae; capitula solitaria vel pauca, raro in capitulescentia corymboidea; folia plerumque integra; phyllaria valde vel leniter concava; flores radii in serie singulari ligulis plerumque albis vel caeruleis; appendices collectentes triangulari-deltatae patenti-pubescentes ramorum styli florum disci; achenia plana 2-nervata eglandulosa; pappus 1(-2)-seriatus setis interioribus teretibus plerumque basaliter caducus plerumque serie brevi externa. Numerus basicus chromosomatum, $x=9$, ad 8,6,5 deminutus. Typus subtribi: *Felicia* Cass.

Herbs or small shrubs, eglandular or commonly stipitate-glandular; leaves entire, rarely toothed or lobed, alternate, opposite in some species of *Amellus*, *Felicia*, *Engleria*, *Poecilolepis*, and *Jeffreya*; heads commonly few or solitary, sometimes loosely paniculate or corymboid (glomerate in *Nolletia* and *Chrysocoma*); phyllaries flat to strongly convex, mostly herbaceous, sometimes with broad scarious margins; receptacles epaleate, paleate in *Amellus* and *Poecilolepis*; ray flowers 1-seriate, sometimes absent, ligules white to blue, yellow in species of *Zyrphelis*, *Nolletia*, *Felicia*, and *Engleria*; disc flowers bisexual, ovaries sterile in *Gymnostephium*, most *Zyrphelis*, and some species of *Felicia*, *Nolletia*, and *Polyarrhena*; disc corollas narrowly tubular, the tube less than half the corolla length; collecting appendages of the disc style branches mostly triangular-deltate, sometimes longer; achenes eglandular (glandular in *Nolletia*), flat, 2-nerved with thickened lateral ribs (glandular, multinerved, and nearly terete in some species of *Chaetopappa*), without glochidiate hairs (except in *Amellus*); pappus 1-seriate or 2-seriate (of bristles and scales in *Amellus*, *Chrysocoma*, *Engleria*, and *Chaetopappa*), basally caducous or persistent, pappus essentially absent in *Jeffreya*. Base chromosome number, $x=9$, reduced to 8,6,5. Species/genera, 184/18.

Felicia group ($x=9$): *Amellus* ($x=9,8,6$), *Chrysocoma* ($x=9$), *Engleria*, *Felicia* ($x=9,8,6,5$), *Gymnostephium*, *Jeffreya*, *Nolletia*, *Poecilolepis*, *Polyarrhena* ($x=9$), *Zyrphelis* ($x=9$).

Lachnophyllum group ($x=9$): *Chamaegeron* ($x=9$), *Lachnophyllum* ($x=9$).

Monoptilon group ($x=9$ or 8):

a. [Europe]: *Bellium* ($x=9$).

b. [North America]: *Chaetopappa* (x=8), *Monoptilon* (x=8).

Pentachaeta group (x=9): *Pentachaeta* (x=9), *Rigiopappus* (x=9), *Tracyina* (x=9).

8. Grangeinae Benth. *in* Benth. & Hook., *Gen. Pl.* 2:176. 1873. Type genus: *Grangea* Adans.

Herbs; leaves often sessile- to stipitate-glandular, commonly pinnatifid to pinnatisect; heads solitary, terminal or axillary, or in a loosely corymboid capitulescence; phyllaries flat, mostly herbaceous, in a few series of nearly equal length; receptacles epaleate (or paleate in 2 genera), often convex; pistillate flowers in several series, ligules absent or about as long as the involucre, white to yellow; disc flowers often with the corolla lobes reduced to 4, commonly with sterile ovaries; disc style branches short, with short, papillate collecting appendages; achenes flat and 2-nerved, sometimes angular, eglandular or glandular, sometimes with glochidiate hairs; pappus absent, of a few short bristles, or a persistent low crown of basally connate scales. Base chromosome number, x=9, reduced (in *Erodiophyllum*) to x=8, and (in *Centipeda*) either raised to x=10 or lowered to x=5. Species/genera, 90/16. A chromosome count of x=11 was early reported for *Cyathocline*, but a number of more recent ones have reported x=9 for two separate species.

Grangea group:

a. [Afro-Asian]: *Ceruana*, *Colobanthera*, *Dacryotrichia*, *Dichrocephala* (x=9), *Grangea* (x=9), *Grangeopsis*, *Grauanthus*, *Gyrodoma*.

b. [Asian]: *Cyathocline* (x=9).

b. [South America]: *Egletes* (x=9), *Plagiocheilus* (x=9).

c. [Australia]: *Centipeda* (x=10), *Erodiophyllum* (x=8).

Nidorella group: *Heteromma*, *Nidorella* (x=9), African "*Conyza*" in part (x=9) (see comments below).

9. Hinterhuberinae Cuatr., Webbia 24:5. 1969. Type genus: *Hinterhubera* Sch.-Bip. *ex* Wedd.

Shrubs, suffrutescent herbs, or herbs, dioecious in *Aztecaster*; leaves resinous-glandular, punctate-glandular with sunken glands, or eglandular, mostly entire, coriaceous, often densely tomentose, alternate, opposite in *Pteronia* and *Olearia*; heads mostly in a corymboid capitulescence; phyllaries flat, herbaceous or variously indurate, evenly thin-scarious in *Novenia*; receptacles paleate or epaleate; ray flowers 1-(2-3)-seriate, ligules long, white or yellow, or the pistillate corollas variously modified or reduced; disc flowers bisexual, sometimes with sterile ovaries (*Diplostephium*, *Oritrophium*, *Novenia*, *Pacifigeron*); disc style branches usually with long, papillate (rarely hairy) collecting appendages; anther thecae basally caudate in some genera; achenes mostly subterete, multinerved, less commonly flat and 2-nerved, commonly glandular, without glochidiate hairs; pappus (1-)2-(-3) seriate, of persistent bristles of more or less even length. Base chromosome number, x=9. Species/genera, 458/29.

Chiliotrichum group (x=9):

a. *Chiliophyllum*, *Chiliotrichopsis*, *Ericameria* (x=9), *Lepidophyllum* (x=9), *Nardophyllum*.

b. *Chiliotrichum*, *Diplostephium* (x=9), *Oritrophium* (x=9).

c. *Llerasia*.

d. *Pteronia*.

Novenia group (x=9): *Novenia* (x=9).

Hinterhubera group (x=9): *Parastrephia*, *Aztecaster*, *Hinterhubera* (x=9), *Westoniella*, *Laestadia*, *Floscaldasia*, *Flosmutisia*.

Madagaster group: *Madagaster*, *Mairia*, *Rochonia*.

Celmisia group (x=9, high polyploid): *Achnophora?*, *Celmisia* (x=9), *Damnamenia* (x=9), *Olearia* in part (x=9), *Pachystegia* (x=9), *Pacifigeron*, *Pleurophyllum*.

Olearia group (x=9): *Olearia* in part (x=9).

Remya group (x=9): *Remya* (x=9).

10. **Lageniferinae** Nesom, *subtr. nov.*

Plantae herbaceae vel leniter suffrutescentes; capitula solitaria vel pauca; flores radii 1-pauciserati ligulis albis vel caeru-

leis; flores disci bisexuales vel saepe ovariis sterilibus corollis saepe 4-lobatis; achenia complanata 2-seriata saepe collum vel rostratum efferentia, saepe glandulosa; pappus plerumque carens. Typus subtribi: *Lagenifera* Cass.

Herbs, sometimes somewhat suffrutescent, rarely low shrubs; leaves entire to dentate or lobed, stipitate-glandular or eglandular, often with strongly reduced vestiture; heads relatively small, few in a loosely paniculate capitulescence (*Rhynchospermum*, *Sheareria*, *Thespis*, and some species of *Myriactis*) or solitary and scapose; phyllaries flat (except *Sheareria* and *Thespis*), often with rounded apices, mostly herbaceous, in 2-3 subequal series; receptacles epaleate, low-convex to flat, sharply conical in "parabellis"; ray flowers in (1-)several series, with white to blue ligules, commonly strongly reduced in length; disc flowers bisexual or often with sterile ovaries; disc corollas 5- or 4-lobed; disc style branches with short, papillate collecting appendages; achenes obovate, flat, 2-nerved (3-nerved in *Sheareria*, 5-nerved in *Thespis*, 6-nerved in "parabellis"), often with a distinct neck or beak, often sessile-glandular, without glochidiate hairs; pappus usually absent or rarely of a few, basally caducous bristles, of persistent bristles in *Lagenithrix* and *Lagenopappus*. Base chromosome number, x=9. Species/genera, 56/12.

Lagenifera group: *Keysseria* (x=9), *Lagenifera* (x=9), *Lagenithrix*, *Lagenopappus*, *Myriactis* (x=9), *Piora*, *Pytinicarpa*, *Solenogyne* (x=9).

Rhynchospermum group: *Rhamphogyne*, *Rhynchospermum* (x=9), *Sheareria*, *Thespis*.

11. **Machaerantherinae** Nesom, *subtr. nov.*

Herbae; capitula pauca vel solitaria; dentes vel lobi foliorum plerumque spinulosi; phyllaria plerumque infra staminei-indurata zona apicali herbacea valde definita; flores radii ligulis plerumque luteis vel interdum albis vel caeruleis; appendices collectentes longi-lanceolatae patenti-pubescentes ramorum styli florum disci; achenia multinervata, strigosa; pappus persistens 2-3(-4)-seriatus setarum teretium vel complanatarum longitudine valde gradatarum. Numerus basicus chromosomatum, x=6. Typus subtribi: *Machaeranthera* Nees.

Herbs; leaves stipitate-glandular or resinous glandular, sometimes eglandular, entire to serrate, uncommonly pinnatifid,

the teeth commonly spinulose; heads few to solitary, rarely in a loose corymboid capitulescence; phyllaries usually in 4-8 strongly graduated series, herbaceous or chartaceous below, commonly with an apical, herbaceous patch, sometimes lightly keeled; receptacles epaleate; ray flowers 1(-2)-seriate, with long, yellow, white, or blue ligules; disc flowers bisexual (functionally staminate in *Benitoa*); disc style branches usually with long, hairy collecting appendages (shorter in the *Xanthocephalum* group); achenes angled, multinerved, commonly short and obconic, eglandular, without glochidiate hairs; pappus 2-3(-4)-seriate, of mostly persistent bristles graduated in length and with a tendency to be flattened, at least basally. Base chromosome number, x=6, reduced to 5,4,3,2. Species/genera, 214/16.

Haplopappus group (x=6,5): *Haplopappus* (x=6,5), *Hazardia* (x=5).

Xylorhiza group (x=6): *Xylorhiza* (x=6).

Machaeranthera group (x=6,5): *Machaeranthera* (x=5,4,3,2), *Oonopsis* (x=5), *Pyrrocoma* (x=6), *Xanthisma* (x=4).

Lessingia group (x=5): *Benitoa* (x=5), *Corethrogyne* (x=5), *Lessingia* (x=5).

Xanthocephalum group (x=6): *Grindelia* (x=6), *Isocoma* (x=6), *Olivaea* (x=6), *Stephanodoria* (x=6), *Xanthocephalum* (x=6), the"phyllocephalus group" (x=6).

12. **Podocominae** Nesom, *subtr. nov.*

Herbae vel aliquando suffruticosae; capitula solitaria vel pauca; folia plerumque dentata vel dissecta, minus plerumque integra; phyllaria valde vel leniter concava; flores radii ligulis plerumque albis vel caeruleis; appendices collectentes lanceolatae patenti-pubescentes ramorum styli florum disci; achenia plana eglandulosa raro nervata in superficiebus; pappus persistens 1-3-seriatus setarum teretium, plerumque serie brevi externa. Numerus basicus chromosomatum, x=9. Typus subtribi: *Podocoma* Cass.

Perennial herbs (rarely annual) or small shrubs, the leaves and stems commonly resinous-glandular; leaves entire or more commonly coarsely toothed to dissected; heads mostly solitary on leafy stems, paniculate in some *Laennecia*, corymboid in some *Tetramolopium*; receptacles epaleate; phyllaries

commonly convex, mostly herbaceous, sometimes with narrow scarious margins; pistillate flowers numerous and in several series, with short, white to bluish ligules (yellow in *Kippistia*); disc flowers bisexual (with sterile ovaries in *Minuria*, *Vittadinia*, a portion of *Tetramolopium*, 2 species of *Ixiochlamys*, *Asteropsis*, *Blakiella*, *Inulopsis*, and *Sommerfeltia*), the corollas narrowly tubular with short lobes, the tube longer than the limb; collecting appendages of the disc style branches mostly short but sometimes long; achenes commonly with glandular surfaces, flat and 2-nerved, often with thickened lateral ribs, the faces with several nerves in *Tetramolopium*, *Camptacra*, and *Vittadinia*, with a tendency to produce a distinct neck (*Asteropsis*, *Dichromochlamys*, *Vittadinia*) or filiform beak (*Blakiella*, *Ixiochlamys*, *Podocoma*), without glochidiate hairs; pappus (1-)2-3 series of basally persistent bristles, the outer series often of much shorter setae, bristles, or squamellae, the entire pappus of lanceolate-deltate scales in the *Elachanthus* group. Base chromosome number, x=9. Type genus: *Podocoma* Cass. Species/genera, 121/18.

a. [South America]: *Asteropsis*, *Blakiella* (x=9), *Inulopsis* (x=9), *Laennecia* (x=9), *Microgynella*, *Podocoma* (x=9), *Sommerfeltia*.

b. [Australasia]:

Ixiochlamys group: *Ixiochlamys*.

Vittadinia group: *Camptacra*, *Dichromochlamys*, *Iotasperma*, *Peripleura*, *Tetramolopium* (x=9), *Vittadinia* (x=9).

Minuria group: *Minuria* (x=9), *Kippistia*.

Elachanthus group: *Dimorphocoma*, *Elachanthus*.

13. Solidagininae O. Hoffm. *in* Engler & Prantl, *Nat. Pflanzenf.* 4(5):145. 1890. Type genus: *Solidago* L.

Homochrominae Benth. *in* Benth. & Hook. [*nom. invalid.*], *Gen. Pl.* 2:174. 1873. See comments below.

Herbs, often suffrutescent; leaves sessile- or punctate-glandular, rarely stipitate-glandular, sometimes eglandular, mostly entire, less commonly serrate; heads in a corymboid capitulescence to secund, paniculate, or solitary; phyllaries flat, commonly basally indurate with a herbaceous apical patch; receptacles epaleate; ray flowers 1-seriate, with ligules yellow, rarely

white, sometimes absent; disc flowers bisexual (ovaries sterile in *Amphiachyris*); disc style branches with short to long, papillate collecting appendages; achenes terete, multinerved, eglandular, without glochidiate hairs; pappus 1-seriate, of persistent bristles, greatly reduced in the *Gutierrezia* lineage. Base chromosome number, x=9, reduced to 8,5,4. Species/genera, 197/19.

Solidago group (x=9): *Nannoglottis*, *Oligoneuron* (x=9), *Oreochrysum* (x=9), *Solidago* (x=9).

Gutierrezia group (x=8,5,4): *Amphiachyris* (x=5,4), *Gutierrezia* (x=5,4), *Gymnosperma* (x=8), *Thurovia* (x=5).

Euthamia group (x=9): *Bigelowia* (x=9), *Chrysoma* (x=9), *Euthamia* (x=9), *Gundlachia* (x=9), *Xylothamia* (x=9).

Chrysothamnus group (x=9): *Chrysothamnus* (x=9), *Stenotus* (x=9), *Vanclevea* (x=9 or 6?).

Amphipappus group (x=9): *Acamptopappus* (x=9), *Amphipappus* (x=9), *Eastwoodia* (x=9).

Bentham's use of the subtribal name "Homochrominae" apparently was intended to establish a contrasting group to his subtribe Heterochrominae Bentham (the latter invalid, without a type or associated genus). The genus *Homochroma* DC. is based on a yellow-rayed species within the predominately white-rayed *Zyrphelis* (Nesom 1994i). Bentham did include *Homochroma* within his Homochrominae, as opposed to the other species of *Zyrphelis*, which he placed in the Heterochrominae, but he did not otherwise associate *Homochroma* with the corresponding subtribal name. This, presumably, was Hoffmann's interpretation, as he proposed the new subtribe Solidagininae and included *Homochroma* among the other genera placed within it. In order to allow continued use of the widely used and validly published Solidagininae, the name Homochrominae must be regarded as invalid.

14. **Symphyotrichinae** Nesom, *subtr. nov.*

Herbae perennes; capitula solitaria vel pauca; folia plerumque integra, minus plerumque serrata; phyllaria plerumque infra straminei-indurata zona apicali herbacea valde definita; flores radii ligulis albis vel caeruleis; appendices collectentes lanceolatae patenti-pubescentes ramorum styli florum disci; achenia multinervata, eglandulosa sparsim strigosa vel glabrata;

pappus persistens 1-seriatus setarum teretium. Numerus basicus chromosomatum, x=9, ad 8,7,6,5,4 deminutus. Typus subtribi: *Symphyotrichum* Nees.

Perennial herbs, rarely annual, 1 species scandent; leaves eglandular or stipitate-glandular in some groups, mostly entire, less commonly serrate; heads in a corymboid capitulescence to secund, paniculate, or solitary; phyllaries flat, commonly basally indurate with a herbaceous apical patch; receptacles epaleate; ray flowers 1-seriate, with ligules white to blue, rarely yellow in *Tonestus*; disc flowers bisexual; disc style branches with lanceolate, hairy collecting appendages; achenes more or less terete and cylindric, multinerved, eglandular (glandular in *Oclemena*), mostly glabrous or glabrate (densely hairy in *Sericocarpus*), without glochidiate hairs; pappus 1-3-seriate, of persistent bristles. Base chromosome number, x=9, reduced to 8,7,6,5,4. Species/genera, 183/13.

Doellingeria group (x=9): *Doellingeria* (x=9).

Eucephalus group (x=9): *Eucephalus* (x=9), *Herrickia* (x=9), *Ionactis* (x=9), *Oclemena* (x=9), *Tonestus* (x=9).

Symphyotrichum group (x=9): *Almutaster* (x=9), *Chloracantha* (x=9), *Oreostemma* (x=9), *Psilactis* (x=9,4,3), *Symphyotrichum* (x=9,8,7,6, 5,4).

Heleastrum group (x=9): *Heleastrum* (x=9), *Sericocarpus* (x=9).

COMMENTS ON THE COMPOSITION OF ASTEREAE SUBTRIBES

1. Asterinae

The Asterinae is primarily restricted to a group of Old World genera that produce white-rayed heads and obovate, flat, 2-nerved achenes with a multiseriate pappus. In *Aster*, *Galatella*, *Crinitaria*, and other species as well, the achenes commonly have glandular faces. Only a single New World genus, *Boltonia*, is included here among the Asterinae. The remaining New World (primarily North American) taxa that have traditionally been placed within the genus *Aster* have terete or subterete, multinerved achenes and are here treated as *Symphyotrichum*, *Doellingeria*, *Heleastrum*, and several smaller genera, all of the subtribe Symphyotrichinae (which see for comments). The genus *Bellis*, which also is commonly placed near *Aster*, is treated in a monotypic subtribe (comments below). The composition and relationships of the Asterinae are discussed in more detail in a separate paper immediately following this one (Nesom 1994k).

2. Baccharidinae

With the hypothesis that dioecy alone cannot define the limits of the group, the Baccharidinae was recently extended beyond the traditionally included New World taxa to encompass a number of others from Africa and southeast Asia (Nesom 1993b). The consistent occurrence of dioecy or related sexual conditions in the New World genera, however, still indicates that they form a monophyletic group. Almost all Baccharidinae are woody perennials (rarely herbaceous) with a strong tendency for a scandent habit; the leaves are often punctate-glandular or resinous or both; heads are small and commonly arranged in a corymboid capitulescence; pistillate flowers are numerous, with corollas reduced (or absent in dioecious groups); central flowers are often with sterile ovaries, the corollas abruptly ampliate, often with long lobes; and achenes are multinerved, terete, and eglandular or sometimes glandular, with a uniseriate pappus of bristles. Three additional genera also appear to be best placed in the Baccharidinae.

The position of *Heteroplexis*

Heteroplexis, endemic to the Guangxi Province of southeastern China, comprises three species characterized by the following features: scandent or trailing herbs with small heads in glomerules; hermaphroditic flowers 4-6, corollas with long, unequal lobes; pistillate flowers 4-7, eligulate; achenes 1.0-1.3 mm long, 6-nerved, apparently somewhat terete; and pappus of barbellate bristles. Each species is known only from the type collection, as noted by Chen (1985), upon whose treatment the present short discussion is based. Zhang & Bremer (1993) placed *Heteroplexis* as a member of the *Erigeron-Conyza* group, noting its similarity in the high ratio of pistillate to hermaphroditic florets. Among the genera they mention, however, this feature is convergent; *Heteroplexis* is not closely related to *Erigeron* or *Conyza*, but Z&B placed *Baccharis* in the same group, and the scandent tendency, closely aggregated disciform heads, long disc corolla lobes, and small, terete, multi-ribbed achenes of *Heteroplexis* do suggest that its evolutionary affinities lie with the Baccharidinae. Other genera of Baccharidinae, as defined here, also extend into southeast Asia, i.e., *Microglossa* and *Psiadia*.

The position of *Commidendron* and *Melanodendron*

Two genera of arborescent Astereae, apparently closely related between themselves, are endemic to the island of St. Helena in the south Atlantic: *Commidendron* (4 species) and *Melanodendron* (monotypic). Although neither finds an easily comfortable position within any of the subtribes treated

here, they are placed in the Baccharidinae on the basis of the following: arborescent habit; leaves minutely glandular and viscid (in *Commidendron*); disc corollas with long lobes (in *Commidendron*); disc style branches with short collecting appendages; anther thecae basally truncate; achenes eglandular, relatively small, multinerved, more or less terete; and pappus 1-seriate, the bristles basally persistent and with dilated apices.

Bentham (1873a) noted that the "nearest connection" of *Commidendron* and *Melanodendron* is with *Diplostephium* (Hinterhuberinae), and their habit, large, coriaceous leaves with pannose indument, corymboid capitulescence, as well as other characters, make this a reasonable assessment. Within the Baccharidinae, however, a woody habit, similar leaves, and corymboid capitulescences are also common, and a pannose indument is characteristic of *Baccharis helichrysoides* DC. and associated species. The geographic position of St. Helena is not unreasonable for isolated members of Hinterhuberinae, but it also lies close to the center of African and South American concentrations of Baccharidinae.

Among the species of *Commidendron*, a conspicuous discontinuity exists between *C. robustum* DC. and the other three. *Commidendron robustum* has leaves densely white-pannose beneath, ligules relatively short and recurving, and solitary heads on long peduncles and arising in pendulous clusters from branch tips. The other species, as well as *Melanodendron*, have less densely pubescent leaves, smaller heads in loose, terminal, corymboid panicles, and longer, spreading ligules. The apparent breadth of this discontinuity, which might be regarded as justification for the establishment of a separate genus, warrants further investigation of the putative monophylesis of *Commidendron*.

Baccharis segregates - *Pingraea* and *Neomolina*

Hellwig (1993) has recently proposed the segregation of two genera from *Baccharis* (*Pingraea* Cass. and *Neomolina* Hellwig) and clearly intends to segregate other smaller groups as well (Hellwig 1990). He has provided evidence that the groups under consideration differ among themselves, especially emphasizing features of vestiture first described in detail by Barroso (1976), but he has not indicated what is gained by dividing *Baccharis* into a number of segregate genera rather than subgenera. With reference to the broader phylogenetic placement of *Pingraea* and *Neomolina*, Hellwig has noted only that (1993, p. 203) "both are related with *Baccharis* L. and certainly closely related to each other." The study of chloroplast DNA variation in the Baccharidinae by Zanowiak (1991) suggests that Hellwig's groups are correctly delimited but also provides evidence that *Baccharis* sensu lato (including *Pingraea* and *Neomolina*) is monophyletic.

3. Bellidinae

Significant features of *Bellis* are the following: rosulate habit, the heads solitary on scapose stems; phyllaries broad and completely herbaceous in few series; receptacles sharply conical; pistillate flowers uniseriate, the rays long, white but often reddish tinged; disc flowers bisexual and fertile, the corollas 5-lobed with a short tube, and with short style branches with deltate collecting appendages; achenes flat, obovate, with a pair of thick marginal ribs, erostrate, the faces short-strigose with straight (non-glochidiate) Zwillingshaare, eglandular; and the pappus absent or represented only by a short, laciniate crown.

Bellis was closely associated with the genera of the Lageniferinae and Brachycominae (as treated here) in Bentham's original description of the Bellidinae (1873b). Hoffmann's enlargement of the Bellidinae (1890) made it considerably more heterogeneous. In DeJong's proposed dissolution of the Bellidinae (1965), he referred the Lageniferinaean genera in question to the Grangeinae (in the present sense) and the Brachycominaean genera to the Asterinae, where he also placed *Bellis*. DeJong (1965, p. 487) noted that *Bellis* is "most closely related to *Bellium* and *Bellidiastrum* in the Asterinae with which it may be placed on the basis of the scapose habit, spathulate toothed or entire radical leaves, herbaceous, biseriate phyllaries, and ribbed achenes which the three genera have in common." Z&B placed *Bellis* with *Bellium* and *Rhynchospermum* into their "*Bellis* group," regarding the first two as sister genera united as "scapose herbs with pauciseriate involucral bracts." As noted below (see Feliciinae), however, the resemblance between *Bellis* and *Bellium* appears to be convergent rather than indicative of close relationship.

Bellis resembles the Brachycominae, Grangeinae, and Lageniferinae in habit, leaf shape, short-tubed disc corollas, tendency to produce short style branches with deltate to nearly truncate collecting appendages, and flat, 2-nerved achenes that are most commonly epappose. The conical receptacles of *Bellis* are similar to those in Brachycominae and Grangeinae. The Brachycominae are similar to *Bellis* in their 1-seriate, relatively prominent ligules and eglandular achenes, while the Lageniferinae and Grangeinae have multiseriate pistillate flowers with reduced ligules and glandular achenes. The latter two subtribes also commonly have 4-merous disc corollas. Thus, despite the overall similarity, *Bellis* cannot be unequivocally associated with any of these three subtribes.

Bellis comprises eight species centered primarily in southern Europe, with several taxa circum-Mediterranean and reaching northwest Africa, Asia Minor, and the Caucasus in their native ranges. *Bellis perennis* L. is adventive in cool-temperate regions around the world. In the present treatment, the genus is regarded as geographically as well as morphologically isolated, although it is similar and probably most closely related to elements of the Brachycominae, Grangeinae, and Lageniferinae.

4. Brachycominae

The most significant features of the Brachycominae are the following: eglandular herbs with few or solitary heads; phyllaries mostly flat, often with broad, hyaline margins; receptacles often conical; ray flowers 1-seriate, with long, white to blue ligules (rarely yellow - Welsh & Reveal 1968); disc flowers bisexual, (ovaries sterile in *Ceratogyne* and some species of *Calotis*), style branches with deltate to triangular, papillate collecting appendages; achenes obovate to oblanceolate, 2-nerved, flat, commonly winged, eglandular, with glochidiate hairs; and pappus usually absent or highly reduced, of 1-2 series of persistent bristles if present. Most of the morphological features of the Brachycominae are rather generalized, but the glochidiate duplex hairs of the achene surfaces are particularly distinctive and characteristic of the subtribe. The genera of the Brachycominae occur in two centers; the center of diversity is in western North America but there are considerably more species in Australia/southeast Asia because of the evolutionary radiation in *Brachycome* (ca. 70 species).

Boltonia has been considered a close relative of North American Brachycominae, based primarily on the common production of conical receptacles (see Beaman 1957 for summary). As discussed in detail (Nesom 1994k), however, *Boltonia* appears to be a member of the Asterinae and hence only distantly related to the Brachycominae. Conical (or distinctly raised) receptacles occur in Asterineaean genera closely resembling *Boltonia* in other features (e.g., *Kalimeris*), and they also occur in parallel in the Grangeinae (at least in some species of *Egletes*) and in several epappose species of *Erigeron* sect. *Olygotrichium* Nutt. (Nesom 1989b).

Numerous species and populations of *Townsendia*, *Brachycome*, and *Calotis* are known to be agamospermic, a tendency that appears to be heritable, at least in this case, and indicative of common ancestry. Within the Astereae, agamospermy is otherwise reported only in *Erigeron* and *Minuria*, genera that do not appear to be intimately related to the Brachycominae. In *Minuria*, the disc flowers are completely sterile while the ray flowers are agamospermic (Davis 1964). Agamospermy is suspected but not demonstrated in *Iotasperma* and *Dichromochlamys* (Nesom 1994g), both closely related to *Minuria*.

When *Aphanostephus* is placed in this phylogenetic perspective, the development of its peculiar, columnar, quadrate-thickened achenes can be viewed as parallel to achenes of some species of *Brachycome*, where the lateral faces are thickened-tuberculate with prominent longitudinal folds (e.g., *B. readeri* G.L. Davis). In both genera, the prominent thickening of the achenial walls is formed late in ontogeny. Further, the "ciliate" pappus of *Aphanostephus* and its tendency to produce deeply lobed leaves can also be found in species of *Brachycome*. On the other hand, the achenes of *A. ramosissimus* DC., which produce a cuplike, upward extension of the achene wall, marginally ciliate with

Zwillingshaare, have a remarkable analog in those of some species of *Grangea* (e.g., *G. maderaspatana* [L.] Poir.), a similarity here hypothesized to be a parallelism reflecting close common ancestry. This putative parallelism also extends to similarities in thickened achenial walls found in some Grangeinae.

In her appraisal of the phyletic position of *Brachycome*, Davis (1948) suggested that its closest relatives are *Astranthium* (the closest) and *Bellis*, emphasizing their shared production of epappose achenes and conical receptacles. Although *Bellis* appears to be somewhat isolated within the Asterinae, it also would be isolated if positioned in the Brachycominae as defined here. Further comments on the position of *Bellis* are found under the Bellidinae (above). Some species of *Brachycome* have highly dissected leaves resembling some in the Grangeinae (e.g., *B. nivalis* F. Muell.), and some have a habit and involucre closely similar to those of *Bellis* (e.g., *B. scapiformis* DC.), but other features of all of these are unmistakenly "brachycomoid," including their winged achenes with glochidiate hairs.

The position of *Ceratogyne*

The monotypic *Ceratogyne* fits well in the Brachycominae in its geography (relatively widespread in southern Australia) and technical characters, particularly its 1-seriate ray flowers and epappose, flat, winged achenes with thickened margins (below the wings) with glochidiate Zwillingshaare along the margins. The "wings" are produced only near the achene apex, forming horn-like processes, whence the generic name. Functionally staminate disc flowers also occur in species of *Calotis*. *Ceratogyne* is specialized in its 1-seriate involucre, tiny heads with few flowers and reduced ligules, and apically elaborated achenial wings. It was regarded as "isolated" by Z&B, but given the diversity and parallel variability that exists within *Brachycome*, it would not be surprising if *Ceratogyne* eventually proved to be a specialized derivative within some group of the latter genus.

Comments on Asian *Calotis* and the status of *Tolbonia*

Calotis comprises 26 species, 24 from Australia and two from southeast Asia. The two Asian species need to be carefully compared to the Australian taxa, but they appear to be congeneric. The taxonomy of the Asian species appears to be as follows:

1. *Calotis anamitica* (O. Kuntze) Merrill, Bull. Soc. Bot. France 77:341. 1930. BASIONYM: *Tolbonia anamitica* O. Kuntze, *Rev. Gen. Pl.* 1:369. 1891. (*Tolbonia* O. Kuntze, *gen. nov., loc. hoc.*).

Calotis gaudichaudii Gaganip., Bull. Soc. Bot. France 68:45. 1921.

2. *Calotis caespitosa* Chang, Sunyatsenia 3:280. 1937.

Calotis anamitica (from Viet Nam, "Anam") has winged achenes with a 1-seriate pappus of 8 retrorsely barbed, awn-like bristles; *C. caespitosa* (from Hunan, China) has unwinged achenes (see Ling *et al.* 1985).

Calotis anamitica (originally *Tolbonia anamitica*), was described by Kuntze as the monotypic *Tolbonia*, the name an anagram for *Boltonia* in reference to the flattened, winged achenes and awn-like pappus. The habit, capitular morphology, sterile disc flowers, and achenial vestiture of these Asian plants, however, places them in *Calotis*. Davis (1952) noted the existence of the Asian species of *Calotis* but did not include them in her treatment of the genus, which was limited to the Australian species. Apparently following *Index Kewensis*, she credited Merrill with sole authorship of *Calotis anamitica* and did not include *Tolbonia* as one of the generic synonyms of *Calotis*. *Tolbonia* was accepted by Z&B (1993) as an isolated genus of the Astereae.

The position of *Geissolepis*

The monotypic *Geissolepis* was transferred to the Astereae by Robinson & Brettell (1972). Lane & Li (1993) reported a chromosome count of n=9 for this species, in contrast to a previous one of n=8 (Ralston *et al.* 1989). The conical receptacles and achenes with glochidiate achenial hairs are distinctive in this genus and indicative of a position among the genera of Brachycominae. Also, the retrorsely barbed achenial awns of *Geissolepis* are found elsewhere in the tribe only in *Calotis*. *Geissolepis* and *Aphanostephus* are apparently the only genera in the subtribe to produce achenes with more than 2 veins: the achenes of *Aphanostephus* have 4(-5) veins, usually 1 in each angle; the achenes of *Geissolepis* also tend to be 4-angled in cross-section but commonly produce 6-8 veins.

The diagnostic glochidiate hairs of the Brachycominae also occur on achenes of *Minuria*. In the latter, however, concave phyllaries, multiseriate ray flowers, disc flowers with long-tubed corollas, tendency to produce short-rostrate achenes, and relatively unreduced pappus of bristles are features that place it in the Podocominae. Analogously, the resemblance between achenes of *Amellus* and some of those in the Brachycominae is striking, but *Amellus* appears to be most closely related to other African genera here placed in the subtribe Feliciinae, as discussed below.

The position of *Townsendia*

Townsendia seems securely placed in the Brachycominae, but it is the only genus within the subtribe with a pappus of essentially unreduced, unmodified bristles, although some species of *Brachycome* produce a whorl of short, awn-like bristles and many *Calotis* produce a few barbellate bristles. The production of a pappus of bristles, however, is an unspecialized condition in the Astereae, especially conspicuous in the Brachycominae and Grangeinae, where there is a strong and persistent tendency for pappus reduction. Recognition of this obviates the necessity of Beaman's conclusion (1957) that the highly reduced pappus of *T. formosa* E. Greene represents the primitive type for *Townsendia*, although his suggestion that this species is phyletically basal in the genus may be correct. *Townsendia formosa* particularly resembles other Brachycominae in two diagnostic features (strongly reduced pappus and conical receptacle), and it is also the only species of *Townsendia* with a rhizomatous, fibrous-rooted habit. Emphasizing the connection of *T. formosa* to the rest of the genus, however, Beaman hypothesized that it is most closely related to *T. eximia* A. Gray, which indeed seems to be closely similar, even in its tendency toward reduction of the pappus.

In its range of habit and leaf shape, *Townsendia* resembles *Amellus* of the Feliciinae. Further, the achenes of *Townsendia*, which are oblanceolate and apically truncate with thickened lateral ribs, resemble those of *Amellus* as much as any of the Brachycominae. The recent description (Dorn 1992) of a species of *Townsendia* with basally caducous pappus places the genus a step closer in its range of pappus variation to *Amellus*.

Townsendia is among the most unspecialized elements in the Brachycominae, judging from its floral and fruit morphology. The evolutionary roots of the subtribe, however, apparently lie in the Southern Hemisphere, where it is part of the grangeoid complex. For this reason, the Brachycominae is regarded here essentially as a Southern Hemisphere group, despite its apparently displaced and disjunct center of diversity.

5. Chrysopsidinae

The characteristics and interrelationships of the genera of Chrysopsidinae have been reviewed in detail (Nesom 1991a, 1991b). In a broader, phylogenetic context, significant features of the subtribe are the tendency to produce a distinctly corymboid capitulescence, disc corollas with enlarged prismatic crystals in the throat, yellow rays, keeled phyllaries (some of which are remarkably similar to those of species placed among the western North American asters of the genus *Eucephalus* and its closest relatives), multinerved achenes, and 2-seriate pappus with the outer series shorter than the inner and usually scaly.

This subtribe is a well-defined natural assemblage except for the genus *Ionactis*, which was earlier included as the most basal member of the goldenaster group (Nesom 1991b) but which now appears to be better placed within the Asterinae (see comments above). All genera of the Chrysopsidinae are restricted to North America except *Noticastrum*. The latter is primarily "austrobrasilien" in distribution, this area proposed as its center of origin (Zardini 1985); a few species occur in central Argentina and one is Andean.

6. Conyzinae

As recognized here, the genera of Conyzinae are relatively generalized in morphology and are characterized as follows: phyllaries, corollas, and achenes with conspicuous orange resin ducts along the veins; disc flowers with fertile ovaries, the corollas mostly narrowly linear with a short tube and erect lobes (somewhat more variable in *Erigeron*); ray flowers multiseriate, the rays mostly white in *Erigeron* and *Conyza* but yellow in some species of *Hysterionica*, *Neja*, *Leptostelma*, *Conyza*, and with three independent derivations of yellow rays in North American *Erigeron* (Nesom 1992d); achenes eglandular, 2-nerved and flattened (multinerved and subterete in *Neja* and *Apopyros*), obovate-oblong, not sharply constricted at the apex, erostrate; and pappus of 1-3 series of bristles in some species of *Leptostelma* and *Neja*, reduced in the others to 1 series of bristles, commonly with a short outer series of setae (but this usually absent in *Conyza*).

Conyza and *Erigeron* have long been associated as close relatives and their phyletic proximity is confirmed in the present study. *Leptostelma*, *Hysterionica*, *Neja*, and *Apopyros* appear to form a natural group marked by a geographic range primarily in southeastern South America, three-nerved phyllaries, and a strong tendency to produce yellow or creamy ligules. There are few technical differences between *Leptostelma*, *Hysterionica*, and *Erigeron* but South American *Erigeron*, as interpreted here, is restricted to Andean (and immediately contiguous) regions; the "austrobrasilien" genera appear to be interrelated among themselves and disconnected from the evolution of typical *Erigeron*. *Neja* has recently been segregated from *Hysterionica* (Nesom 1994c), and *Apopyros* has only recently been recognized (Nesom 1994b). *Leptostelma* has until recently been included in *Erigeron*, but it is justifiably separated (Nesom 1994a), especially if *Hysterionica* is kept apart. Alternatively, all of these would have to be united with *Erigeron*.

Comments on *Erigeron*

The largest Astereaean genus besides *Baccharis* is *Erigeron*, with a worldwide total of more than 400 species. About 240 species of *Erigeron* occur

in continental North and Central America, counting five that are endemic to Central America south of México and about 165 endemic to North America north of México. Of the 93 species of *Erigeron* found in México, 66 are endemic there. The North and Central American species have been divided into 21 sections (Nesom 1989c, 1990c, 1992c, 1994l); broader patterns can be observed among these (Nesom in prep.). An additional 20 species occur in the West Indies and 30 in South America; roughly 110 species occur in the Old World, including the ca. 30 (at least) of subg. *Trimorpha.*

In a series of recent papers, Huber and coworkers have shown that very little differentiation of any kind exists between European and Eurasian alpine species of *Erigeron* (including the generitype, *E. uniflorus* L.; Nesom 1989b), and *Trimorpha* (Huber & Zhang 1991; Huber & Leuchtmann 1992; Huber 1993a, 1993b). They have presented evidence that earlier hypotheses (*e.g.*, Cronquist 1947) for the monophyly of these species are correct, in contrast to a more recent suggestion (Nesom 1989a) that the two taxa should be separated at generic rank. Huber has suggested that the evolutionary derivation of *Trimorpha* from *Erigeron* was perhaps as recent as the Pleistocene.

A situation analogous to this putative origin of *Trimorpha* from *Erigeron* can be seen in the evolution of *Symphyotrichum* subg. *Brachyactis*, which apparently arose from species within *Symphyotrichum* of western North America and subsequently spread into the Old World (Nesom 1994k). The species of subg. *Brachyactis* produce numerous series of both ligulate and eligulate pistillate flowers, while its immediate ancestors produce a single series of ligulate pistillate flowers.

The greatest number of species of *Erigeron* and greatest morphological diversity occur in North America (Cronquist 1947; Nesom 1989b), but the closest relatives of the genus are among the subtribes of the grangeoid complex of the Southern Hemisphere. The apparently ancient isolation of *Erigeron* in North America (primarily the western part of the continent) and its morphologically broad radiation is paralleled by the genus *Ericameria* of the Hinterhuberinae. South American and Old World species of *Erigeron* usually occur in geologically recent (for the most part), high elevation habitats, but it is not clear whether they have migrated into these from North America or represent recent colonizers spreading from restricted, nearby, relictual distributions.

It seems likely that *Trimorpha* and European alpine *Erigeron* (= sect. *Erigeron*) may have originated as sister taxa from a basal element of the genus in Asia, and the North American occurrence of species in both of these primarily Old World groups is secondary. Indeed the monocephalous North American *Erigeron* with European connections are mostly alpine, some are circumboreal, and the nature of their relationship to the rest of the genus, mostly at lower altitudes, is obscure (Spongberg 1971).

In an earlier study (Nesom 1989b), I argued that *Darwiniothamnus* (2 species) of the Galapagos Islands should be retained within *Erigeron*, there be-

ing little besides its peculiar habit and short rays to separate it from *Erigeron*, particularly the species of *Erigeron* sect. *Cincinnactis* Nesom (primarily a Mexican and Central American group). *Darwiniothamnus* is a distinctive element, but if it is held as a segregate genus, several other large and equally discrete North American groups of *Erigeron* would need to be segregated at generic rank.

Status of *Conyza*

Further complicating the definition of *Erigeron* is the unresolved definition of *Conyza* and the nature of its most *Erigeron*-like elements to more typical (generally accepted) *Erigeron*. *Conyza* has consistently been phyletically allied with *Erigeron*. Some African species of *Conyza*, however, have features suggesting they may be most closely related to the *Nidorella* group of the Grangeinae, although another part of African *Conyza* appears to be conspecific with South American (typical) elements of the genus (Nesom 1990b, and see comments under Grangeinae). As understood now, *Conyza* is the only genus of Astereae divided in apparent native distribution between South America and Africa.

Conyza and *Erigeron* subg. *Trimorpha* are similar in their highly reduced pistillate flowers in numerous series, and natural hybrids are known between *Conyza* (*Erigeron*) *canadensis* (L.) Cronq. and *Trimorpha* (*Erigeron*) *acris* (L.) S.F. Gray (Stace 1975). Although these hybrids are rare and appear to be weak and sterile, they recur naturally, indicating that *Conyza* and subg. *Trimorpha* are closely related (see comments in "Intergeneric hybridization in the Astereae" — Nesom 1994k). No hybrids have been reported between *Conyza* and any other species of *Erigeron*, and this may have some bearing on the interpretation of the relationship between subg. *Trimorpha* to the rest of *Erigeron*.

7. Feliciinae

The Feliciinae is primarily an African group, defined here essentially as originally recognized by Grau (1973) and accepted by Z&B, except for the addition of *Engleria*, which was tentatively placed by Z&B as a close relative of *Pteronia*. The genus *Mairia* has been partitioned (Nesom 1994i); the three typical species are placed in the Hinterhuberinae, while the others are treated within *Zyrphelis* of the Feliciinae. Added here to the subtribe are a few extra-African genera of southern Asia, southern Europe, and western North America. In previous classifications (*e.g.*, Bentham 1873b), genera of the Feliciinae have been scattered across several major divisions of the tribe. It is a relatively heterogeneous group, characterized by a herbaceous or suffrutescent habit,

mostly entire leaves, few heads, rays tightly coiling, mostly white to blue (rarely yellow) in a single series, narrowly tubular disc corollas, and eglandular (rarely glandular), flat, 2-nerved achenes with thickened lateral ribs and a 1-2-seriate pappus. The phyllaries, disc corollas, and achenes tend to produce conspicuous orange-resinous ducts in association with the veins.

The position of *Amellus*

Amellus appears to occupy a pivotal position among several groups, with features suggestive of relationship to the Brachycominae and several generic groups placed here within the Feliciinae. Particularly in habit, species of *Amellus* are strikingly similar to some Astereae in western North America, e.g., *Monoptilon* and *Townsendia*. *Amellus* is also similar to *Monoptilon* as well as *Chaetopappa* in its convex phyllaries and biseriate pappus and to Brachycominae in achenial morphology (see comments below with regard to these features). The location of *Amellus* in southern Africa, however, suggests that it is more closely related to *Felicia* and other Feliciinae, as suggested by Grau (1973); in *Amellus*, the uniseriate rays, 2-seriate pappus of bristles and scales, basally caducous in some species, relatively flat receptacles, and tendency to produce opposite leaves support such a placement. All species of *Amellus* have a receptacle with well-developed pales, a feature somewhat scattered through the tribe but also found in the African *Poecilolepis* of the Feliciinae.

Lachnophyllum and *Chamaegeron*

Lachnophyllum (2 species) and *Chamaegeron* (4 species) occur in south-central Asia. They include annual or biennial herbs with an arachnoid-tomentose vestiture and with resinous glands (these sessile in *Lachnophyllum* and apparently responsible for the pleasantly aromatic tendency, stipitate in *Chamaegeron*). Other distinctive features are as follows: heads solitary on long branches in a loosely paniculate capitulescence; phyllaries linear-lanceolate, relatively flat, thin-indurate, and keeled with the raised central vein; pistillate flowers 1-2-seriate, with filiform, coiling ligules; disc flowers few in number compared to the pistillate, the corollas filiform with five, short, recurving lobes, anthers ecalcarate and ecaudate; achenes eglandular, flattened and 2-nerved (distinctly constricted at the apex into a short, broad neck in *Lachnophyllum*); and pappus of few, extremely slender bristles in 1 series (these loosely united at the base in *Lachnophyllum*, but tardily caducous and released separately; in *Chamaegeron*, the pappus bristles are basally connate in an annulus and caducous as a unit). Their base chromosome number is $x=9$.

Lachnophyllum and *Chamaegeron* have been considered Astereaean in previous arrangements of genera within the family, presumably based on their

"*Aster*-like" heads with blue or white, coiling ligules, flat, eglandular, 2-nerved achenes, keeled phyllaries, style branch morphology, and anthers without basal appendages. These two genera are reluctantly placed here within the Feliciinae (based on their geography, linear-lanceolate phyllaries, narrow disc corollas with short, reflexing lobes, and caducous pappus; and there is a tendency for a lightly woolly vestiture at least in some species of *Zyrphelis*), but they appear to be without obvious close relatives. On the other hand, they are similar in habit, vestiture, and aspects of floral morphology to some Inuleae sensu lato, and the possibility of a closer relationship in that direction should be investigated.

The *Monoptilon* group

These plants are particularly characterized by their herbaceous habit, few or solitary heads, persistent, 2-seriate pappus, the inner series of bristles and the outer series of scales; in *Monoptilon* and *Chaetopappa*, the phyllaries are strongly concave, often with broad, scarious margins. Of these two genera, *Monoptilon* is the most similar to African Feliciinae, while *Chaetopappa* is tenuously connected. *Monoptilon* and *Chaetopappa* share a reduced chromosome number (x=8), but most species of *Chaetopappa* have multinerved, fusiform, and nearly terete achenes that are glandular in some species, features unusual in the Feliciinae. *Chaetopappa bellioides* (A. Gray) Shinners, however, has flat, 2-ribbed, obovate, eglandular achenes that are more typical of the subtribe.

The primarily southern European *Bellium* has commonly been allied with *Bellis*, most recently by Z&B, but Bentham (1873b) regarded the two genera as widely separated, and they are indeed disparate in significant features. *Bellis* and *Bellium* are similar in habit, but the latter particularly resembles *Monoptilon* and species of *Amellus* in habit, phyllary morphology, achenes, and pappus. *Bellium* and *Amellus* also are similar in their ligules with an abaxial, purple midstripe, and the former is considered here to provide a geographic and morphological connection between the African elements of the Feliciinae and those of western North America.

The *Pentachaeta* group

The coherence of this small group (ca. 14 species in 3 genera) has been noted by Van Horn (1973) and Robinson & Brettell (1973b). Vigorous artificial hybrids of intermediate morphology have been synthesized between the monotypic *Rigiopappus* and *Tracyina* (Ornduff & Bohm 1975) and the two also are similar between themselves in flavonoid chemistry. The taxa of the *Pentachaeta* group are set apart from the *Monoptilon* group in their combination of annual duration, disc style branches with linear-lanceolate collecting appendages much

mostly entire leaves, few heads, rays tightly coiling, mostly white to blue (rarely yellow) in a single series, narrowly tubular disc corollas, and eglandular (rarely glandular), flat, 2-nerved achenes with thickened lateral ribs and a 1-2-seriate pappus. The phyllaries, disc corollas, and achenes tend to produce conspicuous orange-resinous ducts in association with the veins.

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Lachnophyllum and *Chamaegeron*

Lachnophyllum (2 species) and *Chamaegeron* (4 species) occur in south-central Asia. They include annual or biennial herbs with an arachnoid-tomentose vestiture and with resinous glands (these sessile in *Lachnophyllum* and apparently responsible for the pleasantly aromatic tendency, stipitate in *Chamaegeron*). Other distinctive features are as follows: heads solitary on long branches in a loosely paniculate capitulescence; phyllaries linear-lanceolate, relatively flat, thin-indurate, and keeled with the raised central vein; pistillate flowers 1-2-seriate, with filiform, coiling ligules; disc flowers few in number compared to the pistillate, the corollas filiform with five, short, recurving lobes, anthers ecalcarate and ecaudate; achenes eglandular, flattened and 2-nerved (distinctly constricted at the apex into a short, broad neck in *Lachnophyllum*); and pappus of few, extremely slender bristles in 1 series (these loosely united at the base in *Lachnophyllum*, but tardily caducous and released separately; in *Chamaegeron*, the pappus bristles are basally connate in an annulus and caducous as a unit). Their base chromosome number is $x=9$.

Lachnophyllum and *Chamaegeron* have been considered Astereaean in previous arrangements of genera within the family, presumably based on their

"*Aster*-like" heads with blue or white, coiling ligules, flat, eglandular, 2-nerved achenes, keeled phyllaries, style branch morphology, and anthers without basal appendages. These two genera are reluctantly placed here within the Feliciinae (based on their geography, linear-lanceolate phyllaries, narrow disc corollas with short, reflexing lobes, and caducous pappus; and there is a tendency for a lightly woolly vestiture at least in some species of *Zyrphelis*), but they appear to be without obvious close relatives. On the other hand, they are similar in habit, vestiture, and aspects of floral morphology to some Inuleae sensu lato, and the possibility of a closer relationship in that direction should be investigated.

The *Monoptilon* group

These plants are particularly characterized by their herbaceous habit, few or solitary heads, persistent, 2-seriate pappus, the inner series of bristles and the outer series of scales; in *Monoptilon* and *Chaetopappa*, the phyllaries are strongly concave, often with broad, scarious margins. Of these two genera, *Monoptilon* is the most similar to African Feliciinae, while *Chaetopappa* is tenuously connected. *Monoptilon* and *Chaetopappa* share a reduced chromosome number (x=8), but most species of *Chaetopappa* have multinerved, fusiform, and nearly terete achenes that are glandular in some species, features unusual in the Feliciinae. *Chaetopappa bellioides* (A. Gray) Shinners, however, has flat, 2-ribbed, obovate, eglandular achenes that are more typical of the subtribe.

The primarily southern European *Bellium* has commonly been allied with *Bellis*, most recently by Z&B, but Bentham (1873b) regarded the two genera as widely separated, and they are indeed disparate in significant features. *Bellis* and *Bellium* are similar in habit, but the latter particularly resembles *Monoptilon* and species of *Amellus* in habit, phyllary morphology, achenes, and pappus. *Bellium* and *Amellus* also are similar in their ligules with an abaxial, purple midstripe, and the former is considered here to provide a geographic and morphological connection between the African elements of the Feliciinae and those of western North America.

The *Pentachaeta* group

The coherence of this small group (ca. 14 species in 3 genera) has been noted by Van Horn (1973) and Robinson & Brettell (1973b). Vigorous artificial hybrids of intermediate morphology have been synthesized between the monotypic *Rigiopappus* and *Tracyina* (Ornduff & Bohm 1975) and the two also are similar between themselves in flavonoid chemistry. The taxa of the *Pentachaeta* group are set apart from the *Monoptilon* group in their combination of annual duration, disc style branches with linear-lanceolate collecting appendages much

longer than the stigmatic portions, 1-seriate pappus of bristles, and Californian distribution. The apically clavate Zwillingshaare on the achenes of *Rigiopappus* are unusual and found elsewhere in the tribe in some species of *Vittadinia* but more commonly among genera of the Feliciinae, e.g., *Amellus*, *Felicia*, *Zyrphelis*, and *Gymnostephium* (see illustration and notes in Grau 1971), and it seems likely that, given other similarities, this distinctive specialization marks a close relationship. Van Horn did not consider *Pentachaeta* and *Chaetopappa* to be most closely related between themselves, and the putative relationship of the *Pentachaeta* group to Old World relatives apparently is independent of the *Monoptilon* group.

8. Grangeinae

The Grangeinae is mostly African and Madagascan but, as delimited here, it includes American, Australian, and tropical Asian genera. *Grangea* and *Dichrocephala* extend from Africa and Madagascar into tropical Asia; *Cyathocline* is restricted to tropical Asia; *Centipeda* occurs primarily in Australia, New Zealand, and southeast Asia, with one endemic species in South America, and one species a widespread paleotropical adventive. The strict definition of the subtribe by Fayed (1979) was extended by Z&B to include the Afro-Madagascan *Gyrodoma* (also included earlier by Grau 1977), *Colobanthera*, and *Dacryotrichia*. Further accretion to the Grangeinae of the American *Egletes* and *Plagiocheilus* and the Australian *Centipeda* and *Erodiophyllum* are accepted in the present study. Recently, however, Z&B (1993) placed *Egletes* in their "*Boltonia* group" and *Plagiocheilus* with *Laestadia* and *Floscaldasia*.

Shinners (1949) and DeJong (1965) both observed that the relationship of *Egletes* is with genera centered around *Grangea*. Grau (1977) also noted that *Egletes*, as well as the South American *Plagiocheilus* belong with the Grangeinae. This placement of the two American genera, however, was rejected by Fayed (1979) on technical grounds, although, peculiarly, he included both in his key to genera of Grangeinae. Robinson & Brettell (1973c) correctly positioned *Plagiocheilus* within the Astereae but, looking among South American taxa for its closest relatives, they placed it within a group of genera that are classified here chiefly in the Lageniferinae. While the Grangeinae and Lageniferinae are similar and perhaps closely related to each other (see comment by Grau 1977), plants of the latter tend to produce eglandular herbage, entire or toothed leaves, and beaked achenes glandular at the apex (if glandular) and lacking glochidiate hairs. The two subtribes also are essentially different, but overlapping, in geography.

The position of *Centipeda*

Centipeda has been placed within the Anthemideae in most traditional treatments. Heywood & Humphries (1977), however, accepted it as a member of that tribe only "dubiously." Because it is chemically anomalous in the Anthemideae, Sorensen (1977) suggested that it should be referred to some other tribe; and based on pollen morphology, Skvarla *et al.* (1977) noted that *Centipeda* would be better placed in the Inuleae. Bremer & Humphries (1993) rejected *Centipeda* from the Anthemideae, and, without other comment, suggested that it is a member of the Astereae. Z&B (1993), however, did not include *Centipeda* within their analysis and discussion of the latter subtribe. Bremer (1994) placed it among genera without a clear position in any tribe of Asteroideae.

Centipeda comprises five species that are native to Australia, New Zealand, and southeast Asia in weedy, often wet or moist habitats; one of these, *C. minuta* (L.) A. Br. & Aschers. is adventive more widely through the paleotropics. One other species of *Centipeda* is endemic to southern Chile and adjacent Argentina (Cabrera 1971). An African species originally described as *Centipeda* was transferred to *Dichrocephala.* The genus is briefly characterized as follows: annual to perennial herbs with erect to trailing stems, with glandular-resinous, aromatic herbage, the glands yellowish-resinous, sessile or slightly sunken; leaves coarsely toothed, subclasping, loosely tomentose; heads mostly 4-7 mm wide, cupulate, axillary, sessile or subsessile; phyllaries equal to subequal in 2-3 series, flat and thin-herbaceous; receptacle strongly convex; pistillate flowers eligulate, in numerous (2-8) series; disc flowers relatively few, bisexual, fertile, the corollas short-tubed with 4, wide-flaring, glandular lobes, the style branches short with nearly truncate collecting appendages; achenes persistently glandular, 4-6-ribbed, narrowly clavate to subcylindric, compressed to subterete, the summit of the achene extended into a whitish, cartilaginous crown or shallow cup, epappose.

In its geography and almost all of its technical characters, *Centipeda* fits comfortably within the Grangeinae, where it is particularly similar to *Egletes.* Also, it is remarkable to observe glochidiate hairs on the achenial nerves of *C. cunninghamii* (DC.) A. Braun & Aschers. (though the feature is not consistent within the genus), which further secures its position in the Grangeinae. The 4-6-nerved achenes are unusual, but the elaboration of extra achenial nerves occurs in *Grangea* (cf. *G. zambesiaca* Fayed), and the persistent achenial glands and indurate apex are very similar in appearance to other Grangeinaean achenes. The "U-shaped, inuloid stigmatic areas of the style branches ... unknown in the Astereae ..." described by Bremer (1994, p. 268) appear to be a concomitant of the extreme reduction of the style branches, which are only about 0.05 mm long.

A peculiar aspect of *Centipeda* is its base chromosome number of x=10

(Nishikawa 1985; Gupta 1989, both reporting n=10), which is the only such base number in the entire tribe, unless the number is tetraploid, based on x=5. In either case, the chromosome number is specialized within the Grangeinae and does not bar the admission of *Centipeda*.

The position of *Erodiophyllum*

The Australian *Erodiophyllum* is morphologically specialized, has a reduced chromosome number (x=8), and is a geographical outlier, but it is consistent with other genera of Grangeinae in significant features, including its lyrate-pinnatifid leaves, pistillate flowers in several series with the inner eligulate, the disc flowers with sterile ovaries, and achenes essentially flattened and with a thickened-indurate apex and highly reduced pappus. Grau (1977) observed that the sweeping hairs of the sterile disc flowers in *Erodiophyllum* extend downward past the bifurcation of the branches, a condition shared with two other primarily Australian genera, *Minuria* and *Calotis*, with the implication that these three might be closely related. Variability in South American genera, however, approaches this same condition, as illustrated in Cuatrecasas (1969): *Diplostephium* and *Oritrophium* (Hinterhuberinae), *Baccharis* (Baccharidinae), and *Blakiella* (Podocominae). This feature of stylar morphology is interesting but needs more study before it might be used as an indicator of phyletic affinity.

The *Nidorella* group

The species of the relatively small African genera *Nidorella* (ca. 15 species; Wild 1969a) and *Heteromma* (3 species; Hilliard & Burtt 1973) form a group remarkably similar to typical Grangeinae in most features: herbaceous with leaves often sessile-glandular, entire to toothed, lobed, or lyrate-pinnatifid; heads small, arranged in dense, corymboid clusters; involucral bracts 2-3 seriate; disc flowers bisexual (functionally staminate in *N. undulata* [Thunb.] Harvey), the corollas with short tubes, the style branches short with short, papillate collecting appendages; pistillate flowers absent (*Heteromma*) or in several series, with yellow, reduced ligules (*Nidorella*); achenes small (mostly ca. 1 mm long), flattened and 2-nerved, and glandular on the surfaces; pappus of 1-(2) series of barbellate bristles of equal length and free to the base, basally caducous in *Heteromma*.

Besides the fully developed pappus, generally taller habit, and denser, corymboid clusters of heads in these two genera, there appears to be nothing that would exclude them from the Grangeinae. Further, some typical Grangeinae produce a pappus of barbellate bristles, and some species of *Cyathocline* and *Grangea* closely approach *Nidorella* and *Heteromma* in habit.

Numerous Old World species have been passed nomenclaturally between *Conyza* and *Nidorella* (Wild 1969a, 1969b), and it appears that many Old World *Conyza* may be more closely related to *Nidorella* than to typical (primarily New World) *Conyza* (Nesom 1990b).

9. Hinterhuberinae

The Hinterhuberinae are like the Baccharidinae in their primarily woody habit, although reduction to a herbaceous habit apparently has occurred in a few genera of high elevation or otherwise specialized habitats (e.g., *Oritrophium*, *Laestadia*, *Floscaldasia*, *Novenia*, *Mairia*). All species of the Hinterhuberinae are perennial. The leaves are often punctate-glandular, mostly entire, thick, and often densely tomentose with thin-based hairs; heads are mostly in a corymboid capitulescence; ray flowers are 1-seriate with long ligules; disc flowers are bisexual, sometimes with sterile ovaries; achenes are mostly semiterete and multinerved, less commonly flat and 2-nerved, commonly with glandular surfaces, and with a (1-)2-(-3) seriate pappus.

The Hinterhuberinae was first formally recognized with remarkable insight by Cuatrecasas (1969), but numerous comments in previous literature, beginning at least as early as 1862, have suggested the major outlines of the generic composition of the subtribe, except for a relatively few highly specialized species and genera (see Nesom 1993b, 1993c, 1993e, 1993f, 1994i). Since the most recently proposed, broadened concept of this subtribe, there have been modifications in its composition, primarily in the acceptance of *Laestadia*, *Floscaldasia*, *Flosmutisia*, and *Westoniella* as specialized members of the group (Nesom 1993g, following the suggestion of Cuatrecasas 1986 to expand the group), the proposal to include the monotypic genera *Paleaepappus* and *Aylacophora* within *Nardophyllum* (Nesom 1993e), and the inclusion of a restricted version of *Mairia* (Nesom 1994i). The Hinterhuberinae is remarkable in its pan-temperate distribution in the Southern Hemisphere, where it occurs in Madagascar, southern Africa, South America, and Australasia. Several of the genera occur northward into Central America and México, and one (*Ericameria*) appears to be anciently disjunct in the western United States and adjacent México. The Hawaiian genus *Remya* was positioned near *Olearia* by Wagner & Herbst (1987); after initially rejecting this hypothesis (Nesom 1993b), I return to it as the most reasonable.

The Australasian genus *Olearia* is highly diverse and may prove to be polyphyletic in several directions when investigated from a broader perspective. Drury (1969) and Given (1973) have noted that two groups of New Zealand species of *Olearia* would be better positioned outside of *Olearia*, closer to *Celmisia*. A monotypic genus of the *Celmisia* group (*Pacifigeron*: Nesom 1994j) has recently been described from the island of Rapa in French Oceania, about 4000 kilometers removed from its closest relatives.

The position of *Novenia*

A distinctive species of high elevations in the Peruvian Andes has recently been recognized as the genus *Novenia* (Freire 1986; Freire & Hellwig 1990) (= *Novenia acaulis* [Wedd. *ex* Benth.] Freire & Hellwig). This species has traditionally been placed in the Inuleae-Gnaphalinae (as *Gnaphalium*, *Mnioides*, or *Lucilia*); Freire (1986) also retained it within the "*Lucilia* group" as an isolated genus. Anderberg (1989), however, did not accept it there, noting that it presumably has its closest relatives near genera of the Inuleae sensu stricto; he later (1991) listed it as "Subfamilia Asteroideae incertae sedis." Bremer (1994) also included it among the very few genera of completely unknown position in the subfamily Asteroideae.

Novenia is briefly characterized as follows: small cushion plants, each individual ca. 2-3 cm wide; leaves linear-lanceolate, rigid, glabrous, spreading-recurving, with 3 deep, parallel grooves along entire adaxial surface, smooth beneath, with axillary tufts of white tomentum emerging from base; heads sessile in central clusters, erect, cylindric; phyllaries in ca. 3 series of equal length, 10-12 mm long, oblong-lanceolate and apically attenuate, flat, thin, white-scarious and somewhat translucent, even-textured with no indication of a divided stereome, with a thin, yellowish midvein; receptacle with reduced pales subtending the inner flowers; disc flowers functionally staminate, the style branches linear-lanceolate, without stigmatic lines; pistillate flowers eligulate; achenes oblanceolate, erostrate, 2.5-3.0 mm long, somewhat compressed, with (5-)6, whitish, vascularized, raised nerves, sparsely strigose with filiform, apically acute Zwillingshaare, eglandular; pappus of 2-3 series of persistent, apically attenuate barbellate bristles of equal length; and chromosome number of n=9.

Plants of *Novenia* are highly reduced and specialized in vegetative, phyllary, and floral morphology, but their anthers, achenes, pappus, and chromosome number are Astereaean. Further, a suite of characters places *Novenia* within the subtribe Hinterhuberinae: rigid leaves, axillary tufts of tomentum, receptacular pales, modified or reduced pistillate corollas, functionally staminate disc flowers, multinerved achenes with characteristic Zwillingshaare, and a multiseriate pappus of persistent bristles. The closest relatives of *Novenia* within the subtribe are uncertain, but it is geographically close to a number of other Hinterhuberinaean genera.

The position of *Achnophora*

A position for the monotypic *Achnophora* within the Astereae has been generally recognized, although its infratribal relationships have not. It was treated by Z&B as "isolated" and is tentatively placed here in the subtribe Hinterhuberinae, where it appears to be highly specialized, resembling *Celmisia* in

and the loose capitulescence of non-monocephalous lageniferoid taxa is different from the capitulescence of some Grangeinae, which tends to be corymboid and more compact. Compared to the Brachycominae, the Lageniferinae differ in their multiseriate pistillate flowers, and apically glandular and often rostrate achenes lacking glochidiate hairs. The peculiar, New Caledonian *Pytinicarpa* has 1-seriate pistillate flowers and sharply conical receptacles, but it seems closer to the Lageniferinae than the Brachycominae (Nesom 1994h).

11. Machaerantherinae

In a broad context, significant features of the subtribe Machaerantherinae are the tendency to produce a corymboid capitulescence (in some genera, especially the *Xanthocephalum* group), keeled phyllaries with an apical herbaceous patch, disc corollas (in some taxa, particularly *Grindelia*, *Xylorhiza*, and a few others) with enlarged prismatic crystals in the throat, yellow rays, consistently multinerved achenes, and pappus of 2-4 series of terete to rigidly flattened bristles. The Machaerantherinae (x=6) is the only subtribe in the Astereae with a base chromosome number other than x=9.

The composition of this subtribe appears to be well-defined (Morgan 1990; Morgan & Simpson 1992); the *Lessingia* group is added in the present paper (see notes below). The *Xanthocephalum* group is centered primarily in México and has a relatively clear circumscription. Within the latter, the "phyllocephalus group" (a generic-level taxon) comprises three yellow-rayed, annual species primarily of the south-central and southwestern United States, with a base chromosome number of x=6. These species were recognized by Hartman (1976) to be worthy of generic rank and were recently noted (Hartman 1990) to be "currently under study" by Hartman & Lane. The monotypic *Prionopsis* has recently been incorporated into *Grindelia* (Nesom *et al.* 1993). The composition of *Machaeranthera* (sensu Hartman 1990) is subject to different interpretations. Hartman has followed a relatively broad concept, but the molecular data of Morgan & Simpson indicate that the sections of *Machaeranthera* are cladistically intermixed with *Oonopsis* and *Pyrrocoma*. The North American taxa formerly included in *Haplopappus* have been dispersed across a wide diversity of genera (summary in Nesom & Morgan 1990).

Within the Machaerantherinae, *Grindelia* and *Haplopappus* (sensu stricto) are the only genera with species outside of North America. The latter is restricted to South America, if *Hazardia* is considered separate from it (Clark 1979; Brown & Clark 1982); the South American species of *Grindelia* appear to be closely interrelated and are primarily Andean in distribution (Cabrera 1931).

The *Lessingia* group

Three genera that have not previously been included as close relatives of *Machaeranthera* are added to the subtribe: *Lessingia*, *Corethrogyne*, and *Benitoa* (the *Lessingia* group). There are similarities in their reduced chromosome number (x=5), vestiture of stipitate glands and arachnoid-woolly hairs, loosely paniculate capitulescence of long-pedunculate heads, phyllaries in numerous strongly graduated series and with a sharply delimited, herbaceous apical patch, tendency to produce both white/pink and yellow corollas, achenes multi-nerved, plump, and more or less obconic, and a multiseriate pappus of slightly flattened bristles of different sizes and lengths. Both Hall (1928) and Keck (1956) reasonably compared *Benitoa* to the genus *Croptilon*, here placed in the Chrysopsidinae, but the phyllary and pappus morphology of the *Lessingia* group are particularly indicative of a closer relationship with the Machaerantherinae. It seems clear that these three taxa constitute a natural group within the subtribe, marked by their similarities in vestiture and habit, production of "tack-shaped" glands with large, multicellular heads (particularly on the phyllaries), tendency to produce highly abbreviated collecting appendages of the disc style branches, mottled achene surfaces, and primarily Californian geographic distribution.

Lane (1993b) enlarged *Lessingia* by including the genera *Corethrogyne* (as a single, variable species, citing an unpublished study of the genus by Saroyan, Parnell, & Strother) and *Benitoa* (monotypic, morphologically uniform), but she provided the nomenclatural transfers (1993a) with only abbreviated comments in justification of her departure from tradition. Her rationale emphasized the monophyly of the group, as morphologically apparent, and its apparent isolation from other North American genera, based on her yet unpublished molecular studies of the tribe. While the assignment of rank to these three taxa is somewhat subjective, I believe that it is pragmatically desirable and reasonable as well as phenetically and phylogenetically defensible to maintain both *Corethrogyne* and *Benitoa* as separate genera. Their monophyly with *Lessingia* does not argue that all should be amalgamated into a single genus.

Benitoa, a narrow endemic, is the most recently named of the three genera; Keck (1956) extracted the species from within the heterogeneous North American *Haplopappus* and raised it to generic rank. *Corethrogyne* and *Lessingia*, however, have been recognized as separate genera for a century and a half. Further, the morphological distance that separates these taxa, especially *Benitoa* from the others, is at least equivalent to that between other accepted genera or generic-level taxa of Machaerantherinae known to be closely related (e.g., *Olivaea* and *Grindelia*, *Isocoma* and "the phyllocephalus group").

Lessingia (sensu stricto) produces discoid heads (ray flowers absent) with the outermost tubular flowers bilateral with ray-like extensions, and it is clear that this group is monophyletic without the inclusion of *Corethrogyne* or *Beni-*

toa, both of which are more primitive in the production of typically ligulate ray flowers. The ray flowers in *Corethrogyne* are sterile and epappose and the disc corolla lobes are relatively short, but other differences between it and *Lessingia* are relatively few, and *Corethrogyne* can reasonably be regarded as the sister group of *Lessingia*. The distinctiveness of *Benitoa*, however, was underemphasized by Lane: it has fertile ray flowers with broad, yellow ligules of typical Astereaean morphology, functionally staminate disc flowers (with corresponding loss of stigmatic lines on the style branches), disc corollas markedly constricted at the throat, the anthers above the constriction on long filaments (vs. corollas without a marked constriction, the anthers born on much shorter filaments in *Lessingia* and *Corethrogyne*), 3-nerved achenes (vs. mostly 5-8 nerved) with a greatly narrowed pappus insertion, and a pappus of only ca. 3-8 quickly caducous bristles (vs. pappus of numerous, 2-3-seriate, and relatively persistent bristles in *Corethrogyne* and *Lessingia*, sometimes modified to awns in *Lessingia*). While *Benitoa* is highly specialized (autapomorphic), it apparently occupies an evolutionary position coordinate with both *Corethrogyne* and *Lessingia*.

12. Podocominae

Subtribe Podocominae is recognized by the following characteristics: tendency to produce divided leaves with sessile-glandular vestiture; linear-lanceolate phyllaries, sometimes concave; pistillate flowers in several series, with short, mostly white ligules (variably yellow or white in *Kippistia*, long in *Asteropsis*); disc corollas narrow with the tube much shorter than the limb; achenes flat and 2-nerved (with multi-nerved faces in some of the Australian taxa), commonly with glandular surfaces, with necks or beaks in *Podocoma*, *Blakiella*, *Asteropsis*, *Ixiochlamys*, and *Dichromochlamys*; and the pappus commonly with several series of bristles, sometimes reduced to one series, sometimes also with a shorter outer series. The disc flowers have sterile ovaries in *Blakiella*, *Asteropsis*, *Sommerfeltia*, *Inulopsis*, *Minuria*, a portion of *Tetramolopium*, and two species of *Ixiochlamys*.

As recognized here, this subtribe is divided between Australia and South America. Most of the South American taxa have an austro-brasilien distribution. *Blakiella* and *Laennecia*, however, are wholly or partly Andean; the latter is centered in México and extends as well into the southwestern United States. *Blakiella* is restricted to the páramo region of Venezuela and Colombia (Cuatrecasas 1969), and in its glandular herbage and obovate achenes, it more closely resembles *Sommerfeltia* and *Laennecia* than *Podocoma*, where it was originally placed. *Podocoma* sensu stricto has recently been enlarged (Nesom & Zanowiak 1994) by the addition of two species previously treated as *Conyza*. The status of *Asteropsis*, *Microgynella*, and *Sommerfeltia* is dis-

cussed separately (Nesom 1994e; Nesom & Zanowiak 1994); the taxonomy of *Inulopsis* has been summarized (Nesom 1994d).

Laennecia (Podocominae) is one of only two genera of Astereae (*Conyza* the other) which has single species distributed more or less continuously between South and North America (Nesom 1990a). *Laennecia filaginoides* DC., *L. gnaphalioides* (Kunth) Cass., *L. sophiifolia* (Kunth) Nesom, and *L. schiedeana* (Less.) Nesom occur at relatively high elevations in what appear to be native habitats from Andean regions through Central America and into northern México and the southwestern United States. The genus has two centers of diversity, one in the northern Andes and one in the cordillera of northwestern México.

Species of *Laennecia* have been placed in the Conyzinae, but plants of the latter subtribe differ from those of the Podocominae particularly in their strongly developed orange resin canals in the phyllaries, corollas, and achenes, 3-nerved phyllaries (except much of *Erigeron*), short-tubed disc corollas, eglandular and erostrate achenes, and reduced number and series of pappus bristles. Zhang & Bremer (1993) placed *Podocoma*, *Blakiella*, *Microgynella*, and others in their "*Hinterhubera* group."

The status of *Asteropsis*

Asteropsis macrocephala Less. was treated as a synonym of *Podocoma* by Bentham (1873) but accepted as an independent genus by Baker (1882) and Hoffmann (1890). Grau (1977) regarded it as a synonym of *Podocoma*, a position apparently followed in the recent phylogenetic analysis and classification by Z&B. If treated within *Podocoma*, this species would have to be set apart from all of the others, differing in its combination of stems simple or 1-2 branched near the apex, densely arachnoid vestiture, entire, linear, non-clasping, densely arranged leaves, and large, mostly solitary heads, linear-lanceolate phyllaries in 4-5 slightly graduated series, multiseriate, fertile ray flowers with long ligules (apparently white), disc flowers with sterile ovaries, and large (4-5 mm long), broadly obovate achenes with strongly thickened marginal ribs, a distinctively short-beaked apex, and sericeous, eglandular faces and margins. Instead, *Asteropsis*, which is restricted to southern Brazil and adjacent Uruguay, appears justifiably treated as an independent genus (Nesom & Zanowiak 1994).

Sommerfeltia is ditypic

In an earlier discussion of *Sommerfeltia* (Nesom 1994e), I suggested that *S. cabrerae* Chebat. could not be maintained within *Sommerfeltia*, but after study of authentic specimens (*Castellanos 17.876* [LIL]; *Chebataroff 4500* [LP

isotype]), I conclude that the original assessment of this species is indeed correct and that *Sommerfeltia* is ditypic. *Sommerfeltia* is briefly characterized as follows: perennial herbs from branching, woody caudex; stems, leaves, and phyllaries densely stipitate-glandular, without arachnoid vestiture; leaves stiff, linear, the midrib strongly raised abaxially, with revolute margins, densely arranged along the stems; stems distally branched and bearing several heads in a loosely paniculate-corymboid capitulescence, sometimes monocephalous; phyllaries carinate, thick and strongly indurate, without orange venation, in 3-4 series graduated in length; rays white, in a single series; disc flowers with sterile ovaries, the style branches long-acute with collecting hairs from base to tip, lacking stigmatic lines; achenes flat, 2-nerved, narrowly obovate with apically confluent margins, erostrate, densely strigose-sericeous on faces and margins, or mostly on the margins, the faces glandular; and pappus of 2 series of whitish bristles, without a differentiated outer series. *Sommerfeltia cabrerae* differs from *S. spinulosa* (Spreng.) Less. primarily in its entire leaves (vs. pinnately dissected, with linear lobes) without spinulose apices and its achenes strigose-sericeous on the faces and margins (vs. at the base and along the margins).

In the summary comments on *Sommerfeltia* (Nesom 1994e), "*Rhabdanthus*" was mentioned as a close relative. This was a mistake, as that name will not be validly published.

The status of *Ixiochlamys*

Dunlop (1980a, 1980b) noted that in Australia *Ixiochlamys* (four species, sensu Dunlop) could only be related to *Dichromochlamys* (monotypic); otherwise, it is isolated among Australian Astereae. The species of *Ixiochlamys* are united by their filiform-beaked achenes, but they are disparate among themselves in a number of features, with considerably more accumulated variation than occurs within related genera with a larger number of species. The species of *Ixiochlamys* vary from annual herbs to perennial subshrubs, with leaves entire to highly dissected and with glandular or eglandular surfaces, ovaries of the disc flowers sterile or fertile, and achenes glandular or eglandular. Dunlop (1980b, p. 242) noted that "Within *Ixiochlamys*, *I. filicifolia* and *I. nana* stand together; both are annual with similar foliage and both have fertile disc florets. *I. cuneifolia* and *I. integerrima* are not closely related to each other or to the above species." Further study in a broader context (including South American Podocominae) is warranted to determine if *Ixiochlamys* is monophyletic.

The *Elachanthus* group

Two small genera endemic to southern and southwestern Australia appear to constitute a monophyletic group: *Elachanthus* (ditypic) and *Dimorphocoma* (monotypic). They are characterized as follows: eglandular, annual herbs; leaves entire, linear in *Elachanthus*, oblanceolate in *Dimorphocoma*; heads few-flowered, terminal and solitary; involucre paucibracteate; disc flowers with sterile ovaries, the corollas with 3-4 lobes; ray flowers in 1-several series, white, ligules strongly reduced or absent; fertile achenes 2-veined and essentially flattened (Bruhl & Quinn 1990), strigose-sericeous, without glochidiate hairs; pappus of lanceolate scales in several series, sometimes slightly caducous, or of scales and bristles in *Dimorphocoma*, the pappus of the sterile achenes in both genera usually reduced and only of bristles.

The similarity of *Dimorphocoma* to *Minuria* was early noted by Black (1929), and the relationship of the *Elachanthus* group also has recently been suggested to lie most closely with *Minuria* (see Bruhl & Quinn 1990 for summary). Similarly, the group is here subsumed within the Podocominae. Various aspects relating to the Australasian genera of Podocominae have been discussed in detail in connection with the description of the new genera *Peripleura* (Nesom 1994f) and *Iotasperma* (Nesom 1994g).

13. Solidagininae

The Solidagininae, as recently reviewed (Nesom 1993a), is essentially restricted to the Northern Hemisphere. The plants are herbaceous, sometimes suffrutescent, with mostly entire, usually punctate-glandular leaves, corymboid capitulescence (or variously modified), ray flowers 1-seriate, mostly with yellow ligules, achenes terete, multinerved, and eglandular, and pappus 1-seriate, usually of persistent bristles. The subtribe comprises (1) two loosely associated generic groups of the western United States, the "*Amphipappus* group" and the "*Chrysothamnus* group," (both of these formerly placed together as the "*Petradoria* group," but the genus *Petradoria* is now subsumed within *Chrysothamnus*), (2) the "*Gutierrezia* lineage," with two subgroups primarily of the eastern U.S., the "*Gutierrezia* group" and the "*Euthamia* group," and (3) a number of more loosely associated basal elements: *Solidago*, *Oligoneuron*, *Columbiadoria*, *Oreochrysum*, and *Nannoglottis*. *Tonestus* was placed in the Solidagininae by Nesom (1993a) but is here included within the closely related Symphyotrichinae.

The position of *Vanclevea*

Lane & Li (1993) reported a chromosome count of n=6 for the monotypic *Vanclevea*, in contrast to a previous report of n=9 for the species. Preliminary results of Lane & Jansen (1990) from DNA restriction site data has indicated that *Vanclevea* belongs within the x=6 clade that includes *Xylorhiza* and *Pyrrocoma* (Machaerantherinae), rather than within the Solidagininae, where it is placed in the present treatment. According to Lane & Li (1993, p. 545), the position of *Vanclevea* in the x=6 clade is further supported by "careful observation of technical characters such as disc corolla shape and style branch appendages," and indeed the species was originally named as a species of *Grindelia*, which is closely related to *Xylorhiza* and *Pyrrocoma* and which also has a base chromosome number of x=6. Anderson & Weberg (1974), however, concluded that the closest relatives of *Vanclevea* are the species of *Hesperodoria*, and my own morphological studies (Nesom 1991c) confirmed their observations, suggesting a position for *Vanclevea* among a broader set of genera in the Solidagininae, the "*Petradoria* group." Baird (in prep.), views both *Hesperodoria* and *Petradoria* as members of a redefined version of *Chrysothamnus* (see Nesom & Baird 1993) and *Vanclevea* as most closely related to *Stenotus* and *Chrysothamnus*, or perhaps even included with *Hesperodoria* and *Petradoria* within *Chrysothamnus* (as tentatively accepted and positioned in Nesom 1993a). *Vanclevea* is here regarded as a separate genus of the Solidagininae, with the suggestion that the molecular and chromosomal data need to be re-examined based on yet another sample, in view of the conflicting conclusions regarding its phylogenetic position.

The position of *Nannoglottis*

The nine species of *Nannoglottis* are endemic to south-central China, ranging primarily from Tibet to Yunnan province. They were treated in detail by Ling & Chen (1965), who broadened the genus by consolidating the four species of *Stereosanthus* Franch. and the monotypic *Vierhapperia* Hand.-Mazz. with those two already named in *Nannoglottis* and by describing one additional species of *Nannoglottis*. Ling & Chen followed Hoffmann (1890) by maintaining the genus within the Senecioneae, although they noted its isolated position there. Franchet (1896) noted the possibility of a relationship with the Inuleae. In the original description of *Vierhapperia*, however, Handel-Mazzetti (1937) placed it in the Astereae, noting similarities with species of *Erigeron* (those of subg. *Trimorpha*) and *Conyza*, emphasizing the similarity in eligulate pistillate flowers. Grierson (1964) observed that *Stereosanthus* probably belongs in the Astereae; Grau (1977) reiterated the observation of a similarity between *Nannoglottis* and *Erigeron*; and on the basis of achene anatomy, Jeffrey &

Chen (1984) recently have suggested again that *Nannoglottis* is Astereaean, rather than a member of the Senecioneae. Zhang & Bremer (1993) accepted *Nannoglottis* as a member of the Astereae, although they regarded it as isolated there (without comment).

The central flowers of *Nannoglottis* are functionally staminate and features of the style branches (the stigmatic portions) critical in the interpretation of its tribal position are absent. Even so, *Nannoglottis* appears to be best placed in the Astereae, where it fits comfortably even in microcharacters of flowers and fruits. It is viewed here as a basal member of the Solidagininae, apparently closely related to *Solidago* and *Oreochrysum*. Its connection to *Solidago* can be seen in its leafy habit, the leaves broadly toothed and tending to be basally disposed, its short, yellow, and relatively few ray flowers, disc corollas with deeply cut, reflexing-coiling lobes and abruptly broadened above the tube with the filaments connected at the tube-throat junction, uniseriate pappus with bristles (of the central flowers) apically dilated, and eglandular, fusiform, nearly terete achenes with 8-10 longitudinal ribs.

Nannoglottis is distinguished from all of its putative relatives within the Solidagininae by its trimorphic flowers: the pistillate flowers are of two types, the outer ligulate and few in a single series, the inner eligulate and numerous in several series (both types fertile); the disc (functionally staminate) flowers have sterile ovaries and tubular corollas. Within the subtribe, *Nannoglottis* is further distinguished in its combination of (1) stipitate-glandular vestiture on the stems, leaves, and phyllaries, (2) close, grayish-white tomentum particularly on the lower leaf surfaces, (3) large, basally disposed leaves and clasping cauline leaves, (4) few, relatively large heads in a loose, terminal corymb, (5) completely herbaceous, narrowly oblong-lanceolate phyllaries, and (6) pappus bristles that tend to be basally caducous (though reluctantly). *Nannoglottis* shows remarkable similarities to the monotypic *Oreochrysum* of western North America in its vestiture, large heads, herbaceous phyllaries, and leaf morphology. Each of these two genera is somewhat isolated on its respective continent, but they are hypothesized here to be closely related.

14. Symphyotrichinae

The taxa of Symphyotrichinae are characterized particularly by phyllaries often basally indurate, uniseriate pistillate flowers with white or blue rays, lanceolate collecting appendages of the disc style branches, and terete or subterete, eglandular (mostly) achenes. Most of them produce heads in a corymboid capitulescence, the notable exception being the genera of the *Symphyotrichum* group. Many of the genera of Symphyotrichinae have apically dilated pappus bristles, a feature also found in some Solidagininae but rarely elsewhere in the tribe (except for Baccharidinae), and the pappus elements are

often in 2-3 series. The genera of the *Symphyotrichum* group have a distinctly more diffuse, non-corymboid capitulescence and 1-seriate pappus, the bristles without an apical dilation.

Eleven of the thirteen genera of Symphyotrichinae are segregates from what has generally been recognized as New World *Aster* (Nesom 1994k). *Psilactis* (Morgan 1990) has formerly been included as a section of *Machaeranthera*; *Tonestus* was formerly included within *Haplopappus* (Nesom & Morgan 1990), except for *T. kingii* (D.C. Eat.) Nesom, which was previously identified as *Aster* (Nesom 1991d). The recognition of these North American segregate genera has been occasioned by (1) my conclusion that typical *Aster* and its closest relatives are almost completely restricted to the Old World (characterized by obovate, flattened, 2-nerved achenes commonly with glandular faces) and by (2) the lack of any unifying suite of features that could provide definition to a single, "aster-like" genus in the New World, as it has been mostly conceived until now. A detailed discussion, taxonomic treatment, and accounting of the species of Symphyotrichinae is provided in a separate paper (Nesom 1994k).

The position of *Tonestus* has previously been suggested to be within the Solidagininae (Nesom 1991d, 1993a), and indeed its yellow rays are anomalous in the Symphyotrichinae, but it seems more reasonably placed in the latter in habit, vestiture, and phyllary morphology. *Sericocarpus* also has been most recently suggested to be a member of the Solidagininae (Nesom 1993a), but in a larger perspective, it now appears to me to have been correctly placed by Cronquist (1947) within North American *Aster* sensu lato, where it most resembles *Heleastrum*. The position of *Ionactis* remains somewhat equivocal (see below), but it is treated here within the Symphyotrichinae.

The genera of Symphyotrichinae are mostly restricted to North America, but some species of *Doellingeria* also occur in eastern and southeastern Asia (Nesom 1993h, 1994k). One species group of *Symphyotrichum* has radiated in South America. Both the Symphyotrichinae and Solidagininae, like the Asterinae, have genera (*Doellingeria*, *Solidago*, *Aster*) and pairs of genera (*Oreochrysum*/*Nannoglottis*, *Boltonia*/*Kalimeris*) divided in distribution between Asia and North America.

The position of *Ionactis*

Ionactis was recently hypothesized to be the most primitive member of the Chrysopsidinae (Nesom & Leary 1992), but that subtribe is a well-defined group without *Ionactis*, and it seems unreasonable to add a genus of white-rayed species that lack consistent and diagnostic features of the goldenasters. Nevertheless, the goldenasters may have originated from ancestral stock at least partly resembling *Ionactis*. Significant features of *Ionactis* are the following: stems stipitate-glandular; leaves entire, tending to be linear, densely

arranged on the stems; heads few in a loosely paniculate capitulescence; phyllaries keeled, herbaceous to chartaceous, without a sharply delimited apical zone; rays uniseriate, white to blue; disc achenes 2-nerved and somewhat flattened, glandular in one species, the ray achenes 3-nerved and angular; pappus 2-seriate, persistent, the inner series of bristles, outer of much shorter scales.

The few-nerved achenes of *Ionactis* suggest that it might be better placed within the Asterinae, where it is similar to the Old World genus *Arctogeron* in habit and vestiture. In its distinctly carinate phyllaries, however, *Ionactis* resembles other North American genera, particularly those of the Chrysopsidinae and basal genera of the Solidagininae and Symphyotrichinae. The cauline vestiture of abundant stipitate glands (Type C trichomes) of *Ionactis* also occurs on some genera within these three subtribes, suggesting that all may have arisen from the same genetic nexus.

Ionactis has been compared to *Chaetopappa* (Soreng & Spellenberg 1984), and one species of *Ionactis* has glandular achenes and one has sterile disc ovaries (Nesom & Leary 1992), features similar to those of *Chaetopappa*. In *Chaetopappa*, however, the phyllaries are concave and not carinate, the achenes are mostly subterete, and the two genera have different chromosome numbers. Other contrasting features between the two are detailed in a recent study (Nesom 1992b).

GENERA EXCLUDED FROM THE ASTEREAE

Formania W.W. Smith & J.K. Small.

This monotypic genus (*Formania mekongensis* Smith & Small) from southern China (Yunnan) was placed by its original authors (Smith & Small 1922) near *Chrysanthemum* (Anthemideae), but most recently it has been treated as an isolated member of the Astereae by Zhang & Bremer (1993). According to the original detailed description and illustration, it is "an aromatic shrub of 2-3 feet" with leaves of a thick, papery texture and lobed-incised margins. Each head produces about 8 disc flowers and about 10 ray flowers with pale yellow ligules; the anther thecae bear long tails and the styles are truncate; and the pappus is formed of five, thickened, linear pales with a shorter outer series of more numerous scales. If *Formania* belongs within the Astereae, it is isolated there, although it might be placed as a highly aberrant, geographically isolated member of the Hinterhuberinae. Bremer & Humphries (1993) rejected it from the Anthemideae without suggesting an alternative position. It is possible that *Formania* is a member of the Inuleae sensu lato.

Isoetopsis Turcz.

This monotypic genus (*Isoetopsis graminifolia* Turcz.) is widespread in mainland Australia and Tasmania. The observations of Robinson & Brettell (1973a) and Bruhl & Quinn (1990) have suggested that *Isoetopsis* is phyletically close to *Elachanthus* and *Dimorphocoma* (Podocominae), but it was excluded from the Astereae by Turner (1970), Skvarla *et al.* (1977), and Grau (1977), who were followed by Z&B (1993). Anderberg (1989, 1991) placed it in the Gnaphalieae (subtribe Angianthinae Benth.), its position there seemingly secured by the further observation that it produces a divided stereome, terete but 2-nerved achenes with a pappus of lanceolate, pinnate-reticulately veined scales, and ectomycorrhizae. Its reported chromosome number (x=17; Turner 1970), unknown in the Astereae, is not out of place in the Angianthinae.

Phacellothrix F. Muell.

This monotypic genus (*Phacellothrix cladochaeta* F. Muell.) is endemic to Australia (Queensland and Northern Territory) and Papua New Guinea. The plants are characterized as annual herbs with loosely arachnoid-tomentose vestiture, decurrent leaves, and additional features as follows: heads solitary on long naked peduncles; phyllaries in 5-6 graduated series, with broad, thin-hyaline margins and a basal, glandular-herbaceous portion, fenestrated, with a divided stereome; pistillate flowers absent; disc corollas with lobes cut nearly to the tube; style branches strongly recurving-coiling away from each other at maturity, with linear-lanceolate appendages with long, nearly clavate sweeping hairs; achenes cylindric, 2-nerved, with a ring of white, sessile, bulbous "glands" in a ring at the apex and also scattered over the face, the "glands" myxogenic, sessile, of duplex hairs; and pappus a ring of long, white, linear, apically laciniate scales.

Phacellothrix was accepted by Grau (1977) and Z&B as a member of the Astereae, but in its habit, vestiture, leaf and phyllary morphology, and floral and fruit morphology, it strongly resembles the Australian genus *Rutidosis* DC. (Gnaphalieae sensu Anderberg 1991). Indeed, it has been treated within *Rutidosis* (as the synonym *R. brownii* Benth.), as noted by Bailey (1900), who placed *Rutidosis* and *Phacellothrix* in the same immediate vicinity of his treatment. The latter, however, was not included in Anderberg's monograph of the Gnaphalieae.

Apostates Lander

Lander (1989) separated the French Polynesian *Apostates* from *Olearia* as a monotypic genus and provisionally placed it in the Astereae, noting that it

appears to be isolated there. Given the broad range of seemingly primitive, Southern Hemisphere genera (including *Olearia*) that constitute the Hinterhuberinae, *Apostates* might be a basal member of that subtribe, based on its shrubby habit and coriaceous leaves. In a combination of other significant characters, however, it would be isolated there: decussate leaves with palmate venation; discoid heads (with only tubular, bisexual flowers), corollas abruptly ampliate with lobe sinuses extending nearly to the throat; style branches with truncate collecting appendages; achenes prismatic (4-nerved) with a narrowed, nearly stipitate base; and a 1-seriate pappus of flattened, laciniate scales. I suggested (Nesom 1993b) that *Apostates* might prove to belong in the Inuleae sensu lato, although a possible position for it there also seems obscure.

Apodocephala J. Baker

Apodocephala is a genus of eight species endemic to Madagascar. These have been described and illustrated in detail by Humbert (1960), their morphology summarized by the following account: shrubs or small trees with petiolate, entire to shallowly dentate, coriaceous, punctate-glandular, and often densely tomentose leaves; upper stems, corolla tubes, and achenes stipitate with Type C trichomes; heads cylindric to campanulate, discoid, few-flowered (3-4 flowers per head in six species, 15-20 in one, 6-12 in one), aggregated in glomerules, these spread into a broadly corymboid, terminal capitulescence; receptacles paleate; flowers bisexual, the corollas lacking a limb, with spreading-recurving, linear-lanceolate lobes cut to the apex of the linear tube, the adaxial surfaces densely papillose, the tube and lobes of equal length; anther thecae dark purplish, with white apical appendages, basally caudate; style branches strongly recurving-supinate, with ovate-deltate to linear-lanceolate collecting appendages ca. 1/3-1/5 the length of the branches, the branches internally papillate; achenes semiterete and multinerved to flat and 2-nerved, more or less oblong in outline, with a broadly stipitate base, carpopodium barely if at all developed, the surfaces commonly stipitate-glandular (at least near the apex), without other vestiture; pappus absent.

Following Grau (1977), Z&B and Bremer (1994) have included *Apodocephala* in the Astereae, where they treated it with *Vernoniopsis* as the "*Apodocephala* group." It was not included in their cladistic analysis, because of "insufficient information," but they judged the group to be within their broadly conceived subtribe Asterinae. If placed in the Astereae, however, *Apodocephala* is isolated; the internally papillate style branches, in particular, appear to separate it from that tribe. In habit and some aspects of corolla and fruit morphology, it resembles *Apostates*, although not in style morphology. Its closest relatives might be found among the genera at the base of the Heliantheae sensu Karis (1993b).

Psednotrichia Hiern.

The original species of *Psednotrichia* (*P. tenella* Hiern) is known only from Angola in southwest Africa. It was described as comprising annual, subglabrous herbs with linear leaves in a basal rosette. In addition to the description, Hiern provided a precise illustration of a head, along with floral and achenial details. The heads are discoid (lacking pistillate flowers), with a single series of 8, narrowly ovate involucral bracts. The receptacle is steeply hemispheric. The achenes are brownish and ca. 1.3 mm long ("1/20 poll."), 5-nerved and somewhat terete, the surfaces with numerous, large, sessile-clavate, light-colored papillae (probably modified Zwillingshaare, perhaps myxogenic), and the pappus is a single series of basally caducous, barbellate bristles. The style branches are relatively short, with two separate, lateral stigmatic lines and a truncate apex (apparently appendiculate) with a slender, central protrusion. Additionally, Hiern (1898, p. 290) noted, without any other explanation, that "There are two kinds of flower, slightly differing, one with a less deeply divided corolla than in the other, and with the longer kind of androecium accompanied by the shorter kind of style."

A second species, *Psednotrichia australis* Alston, was described from the Cape Province of South Africa. It has radiate heads and flat, obovate, eglandular achenes and is probably not closely related to the first but rather is more likely a member of the Feliciinae. I have not seen specimens of either species, but in its combination of highly reduced involucre and distinctive style branch morphology, *P. tenella* is anomalous within the Astereae. The achenes and style branch morphology resemble those in some Gnaphalieae, but the uniseriate involucre is peculiar there.

Psednotrichia was apparently first placed in the Astereae by Grau (1977), who remarked (p. 556) that it is "a very doubtful genus and could well be reduced to synonymy on further investigation," but he did not say to what genus he perceived such a close relationship, nor did he mention the difference in the two species. *Psednotrichia* was included in the Astereae by Z&B as an isolated genus.

OVERVIEW OF TRIBAL STRUCTURE AND BIOGEOGRAPHY

A summary of the proposed subtribal structure of the Astereae is shown in Figure 1. In the course of the present study, I have not been able to formulate a meaningful cladistic hypothesis regarding inter-subtribal relationships because of variability in character states, much apparent parallelism among the subtribes (and corresponding difficulty in assessing homology), and problematic decisions regarding inter-generic relationships within the subtribes. The present classification, however, should facilitate the preparation of a more objective, cladistic study of the tribe. Various suggestions and comments regarding the nature of putative relationships are provided in the main text

and in the further discussion below, but I am more confident regarding the generic groupings proposed here than any arrangement that purports to be phylogenetic.

Three main groups of the Astereae are mostly restricted to the Southern Hemisphere: the Baccharidinae, the Hinterhuberinae, and the loosely assembled "grangeoid complex," which includes seven subtribes. A few genera within each of these three groups are endemic to the Northern Hemisphere (primarily in western North America). Outside of the Southern Hemisphere, the remaining subtribes (Asterinae, Symphyotrichinae, Solidagininae, Machaerantherinae, and Chrysopsidinae) are autochthonous in the Northern Hemisphere; all but the Asterinae are largely endemic to North America. The greatest density of genera (number per area) as well as the preponderance of the yellow-rayed taxa in the tribe occur in these North American groups. Some genera and species groups from the Symphyotrichinae, Solidagininae, Machaerantherinae, and Chrysopsidinae have secondarily reached South America. The genera of Asterinae occur in Asia and Europe, but they are most numerous in southeastern and central Asia; one genus (*Boltonia*) of the subtribe is endemic to North America, and one species of *Aster* (*A. alpinus* L.) has secondarily reached North America. The Asterinae is the only subtribe that has radiated in Asia, with the exception of the Solidagininae, in which a few basal elements are disjunct between southeast Asia and North America, and a portion of the Lageniferinae. The Solidagininae, however, is otherwise North American.

The summary diagram (Figure 1) is broadly structured on the following bases. In the Southern Hemisphere, there are three large and morphologically distinct groups, among which the nature of the phyletic relationships is obscure, perhaps reflecting an early diversification from which intermediates have become extinct. The subtribes of the grangeoid complex are united on the assumption that their flattened, 2-nerved achenes are homologous and specialized within the tribe (see below). In the Northern Hemisphere, the four primarily American subtribes appear to be related among themselves and to the other Northern Hemisphere subtribe, the primarily Old World Asterinae. An evolutionary transition between the Hinterhuberinae and the Northern Hemisphere groups is plausible, as noted below.

Within Astereaean subtribes of the Southern Hemisphere, continental disjunctions between South America and Africa-Madagascar (Baccharidinae, Grangeinae, Hinterhuberinae, and perhaps Conyzinae) suggest that these taxa were evolving at least by the middle to late Cretaceous, when such biogeographic interchange would have been possible via continental routes or at least across island bridges that may have persisted for a short while longer. According to Bremer (1993, p. 120), however, "no causal relationship [exists] between continental separation of Africa and South America and the distribution of Asteraceae." This statement is based on his conclusions that "Africa lacks old relict Asteraceae genera. Instead, the original distribution of the Asteraceae

seems to be Pacific." And "there are few sister-group relationships between African and South American Asteraceae, with those found representing individual exceptions rather than parts of more general patterns."

These generalizations formulated by Bremer do not appear to be true for the Astereae. There are "Pacific" patterns in the tribe (see below), but there also is a prominent pattern of African-South American relationship (Figures 2,3,4, and 7). Both the Hinterhuberinae and Baccharidinae have significant numbers of genera and species in Africa, and Madagascar houses genera of both subtribes that might be regarded as relict; both subtribes are abundantly represented in South America. The most primitive members of the Baccharidinae are African and southeast Asian, and putatively primitive Hinterhuberinae are spread across southern Africa, South America, and Australasia. The Grangeinae are centered in Africa, with fewer genera in South America and Australasia.

The origin of the family Asteraceae has been considered to be no earlier than the Oligocene (Raven & Axelrod 1974). Notwithstanding the lack of fossil evidence for a pre-Tertiary origin of the family, the geographic distribution of some Astereae (based on the phyletic patterns hypothesized here) is similar to that of many other families and generic groups known to have a Cretaceous history and hypothesized to be vicariantly divided in the Cretaceous between Africa and South America. Such a view of the age and evolution of the Asteraceae is in agreement with Turner (1977), following perceptive summaries by Bentham (1873a), but not with Bremer (1994), who looks for an "early Tertiary" origin of the family.

The repeating pattern of disjunction between South America and Australasia in the Hinterhuberinae, Grangeinae, Podocominae, and Lageniferinae (Figures 2,4, and 6) suggests that these groups were in existence at least by early Tertiary, as the connection between South America and Australia through Antarctica persisted only until early Eocene. Groups within other tribes of Asteraceae (*e.g.*, Anderberg 1991; Ryding & Bremer 1992) also show a similar circum-Pacific pattern of distribution, as do other specialized angiosperm families (*e.g.*, Goodeniaceae, Myoporaceae, Stylidiaceae).

The patterns of distribution in the Northern Hemisphere groups suggest that the Asterinae and Solidagininae were members of an early Cenozoic, Laurasian temperate forest flora. Migration between southeast Asian and North American elements of this flora was occurring maximally in the Eocene (Tiffney 1985a,b). Finally, the various Southern Hemisphere groups that are now disjunct in western North America probably migrated across the North Atlantic from the Old World in the early Tertiary (see Graham 1993 for a summary). The establishment in North America of the morphologically complex and apparently primitive *Erigeron* (Conyzinae) and *Ericameria* (Hinterhuberinae) from either South American or Old World stock probably was significantly earlier than the southward extrusion (into South America) of species or species

and in the further discussion below, but I am more confident regarding the generic groupings proposed here than any arrangement that purports to be phylogenetic.

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Within Astereaean subtribes of the Southern Hemisphere, continental disjunctions between South America and Africa-Madagascar (Baccharidinae, Grangeinae, Hinterhuberinae, and perhaps Conyzinae) suggest that these taxa were evolving at least by the middle to late Cretaceous, when such biogeographic interchange would have been possible via continental routes or at least across island bridges that may have persisted for a short while longer. According to Bremer (1993, p. 120), however, "no causal relationship [exists] between continental separation of Africa and South America and the distribution of Asteraceae." This statement is based on his conclusions that "Africa lacks old relict Asteraceae genera. Instead, the original distribution of the Asteraceae

3. The grangeoid complex

This complex of seven subtribes is a loosely knit group set apart from the Baccharidinae and Hinterhuberinae as herbaceous, relatively few-headed plants with white rays and 2-nerved, variably glandular achenes. The group may be monophyletic, particularly if the basic achene morphology (flattened, 2-nerved) proves to be homologous among its various constituents and specialized within the Astereae. Tribes closely related to the Astereae and possibly retaining ancestral features (Anthemideae, Gnaphalieae, Inuleae, Senecioneae - see Karis 1993a) produce achenes that are mostly terete and multinerved. Although a number of caveats are proffered in the foregoing discussion (and related discussions in some of the separate papers), the limits of most of the grangeoid subtribes appear to be relatively clear.

The Grangeinae are spread across Africa, South America, Australia (*Erodiophyllum* and *Centipeda*), and southeast Asia (*Cyathocline*). The phyletic position of *Erodiophyllum* may be subject to different interpretation and needs to be investigated in more detail. The division of the Podocominae and elements of the Lageniferinae, however, between South America and Australia confirms the possibility of such a distribution. There are wide disjunctions within the Brachycominae between Australia and western North America and within the Feliciinae between Africa and western North America.

Erigeron, the largest and one of the most morphologically complex genera in the grangeoid complex, appears to be largely autochthonous in North America. At least it is clear that the greatest diversity, by far, in the genus occurs there, but distinct groups also occur in Asia (sect. *Erigeron* and subg. *Trimorpha*) and South America, and the closely related *Conyza* appears to be divided between South America and Africa (see discussion of the Conyzinae). Apart from these, the closest relatives of *Erigeron* are hypothesized to be the members of the *Leptostelma* group (Conyzinae) of southeastern South America, which suggests that *Erigeron* arose from basal stock from that area. It is conceivable, however, that *Erigeron* arrived in North America from Africa rather than from South America, given the apparent ties between Africa/central Asia and western North America (see notes on Feliciinae). In fact, this conceivably could also have been the pathway of migration for the widely disjunct Brachycominae as well as for the genus *Ericameria* (Hinterhuberinae), which is analogous with *Erigeron* in its internal complexity, inextricable relationship to Southern Hemisphere taxa, and geographic isolation.

As noted in the discussion of the Bellidinae, evidence suggests the subtribes Grangeinae, Brachycominae, and Bellidinae, and possibly the Lageniferinae, are closely related. The glochidiate hairs that are diagnostic of the Brachycominae also occur in the Grangeinae, and the relationship between these two groups appears to be perceptibly close. The nature of the phyletic connection of the Feliciinae, Conyzinae, and Podocominae to the rest of the grangeoid

complex is more obscure.

Northern Hemisphere

The primarily North American subtribes Solidagininae, Symphyotrichinae, Machaerantherinae, and Chrysopsidinae are distinguished in part by their combination of mostly eglandular, multinerved, and fusiform-cylindric to obconic, more or less terete achenes. The Asterinae, in contrast, produce obovate achenes that are 2-nerved (laterally) and strongly flattened, commonly with glandular faces. The Asterinae pappus commonly is biseriate, sometimes with several series of bristles but often with inner bristles and a short outer series of scales; less commonly, it is reduced to a single series of bristles. In these features, as well as the distinctly corymboid capitulescence of many of the genera, the ancestry of the Asterinae and American subtribes is most reasonably sought among species similar to those placed here within the Hinterhuberinae. Species of the Baccharidinae and the grangeoid complex are generally too specialized to be considered as ancestors of any of the Northern Hemisphere groups, or at least their specializations obscure the detection of a close relationship. Achenes of Hinterhuberinae appear to be basically terete and multinerved with a multiseriate pappus; thus the flattened Asterinaean achenes probably are specialized, their shape derived independently from those of the grangeoid complex.

The Solidagininae and Symphyotrichinae are similar in their mostly slender, cylindric, and eglandular achenes and show other similarities between putatively basal elements in each group: *e.g.*, disc corollas abruptly ampliate at the tube/throat junction, with relatively long, reflexing-coiling lobes and papillate (vs. hairy) collecting appendages of the style branches; pappus bristles apically dilated. Both subtribes have elements in both eastern and western North America; genera in both subtribes are disjunct between North America and southeastern Asia.

The Machaerantherinae and Chrysopsidinae appear to be primitively yellow-rayed groups, and both groups have biseriate or multiseriate pappus. The large, distinctive crystals of the disc corollas that are diagnostic of the Chrysopsidinae also are characteristic of a few genera of the Machaerantherinae, and it seems reasonable to hypothesize that the two groups are closely related, their point of common ancestry evidently lying near the divergence of the Symphyotrichinae and Solidagininae. Both the Machaerantherinae and Chrysopsidinae are restricted to the New World. The Machaerantherinae is a group of western North America, with an outlying genus (*Haplopappus*) in Andean South America. The Chrysopsidinae is a relatively small subtribe but extends completely across North America and south through México into Guatemala; it also has a South American outlier, *Noticastrum*.

Ionactis, *Erigeron*, *Sericocarpus*, *Heleastrum*, and *Symphyotrichum* are divided in native range between eastern and western North America; *Solidago* and *Euthamia* are primarily eastern genera with a few representatives in the west, while the situation is reversed in *Heterotheca*. Other North American genera of Astereae are essentially restricted to either the eastern or western part of the continent.

The concentration of Southern Hemisphere disjuncts in western North America has already been mentioned in several contexts. At least four subtribes appear to be represented in this pattern: Hinterhuberinae (*Ericameria*, from South America or the Old World); Conyzinae (*Erigeron*, probably from South America); Brachycominae (4 genera, from Australia); and Feliciinae (the *Pentachaeta* group with 3 genera, from Africa; and the *Monoptilon* group with only *Monoptilon*, from Africa. The origin of the isolated *Chaetopappa* may also prove to be similar. The distribution pattern of these generic groups suggests that they are part of the floristic assemblage that comprises many primarily woody genera common to the Mediterranean and Californian regions: e.g., *Arbutus*, *Platanus*, *Populus*, *Rhamnus*, *Rhus*, and *Styrax*. These plants apparently moved westward across North Atlantic connections between North America and the Old World during the Late Cretaceous to Early Eocene (Raven 1971; Raven & Axelrod 1974). An analogous pattern of amphi-Atlantic temperate disjunctions in the Northern Hemisphere has been observed for more tropical taxa of North and Central America, the New World extensions of the "the boreotropical flora" (Wolfe 1975; Tiffney 1985a, 1985b). The generality of this pattern has recently been amplified by addition of other examples (Lavin & Luckow 1993).

Species and species groups of several primarily North American genera occur in South America: one species of *Psilactis* (Symphyotrichinae) in the northern Andes, one species of *Solidago* (Solidagininae) mostly in southeastern South America but now expanding its range, groups of *Gutierrezia* (Solidagininae) and *Grindelia* (Machaerantherinae) primarily in the central and southern Andes, and *Laennecia* (Podocominae) with several species scattered far down the Andes and one species group autochthonous in the northern Andes. The few species of *Laennecia*, one of *Psilactis*, and several of *Conyza* are the only ones of seemingly native occurrence that occur in a more or less continuous distribution between North and South America. Compared to *Noticastrum* and *Haplopappus*, the establishment of these primarily North American genera (*Psilactis* and *Laennecia*) in South America was probably much later.

SIGNIFICANT REMAINING PROBLEMS IN ASTEREAE CLASSIFICATION

Interesting problems for investigation abound within the Astereae. Intergeneric and inter-subtribal relationships remain to be studied, including those

hypotheses presented here regarding the composition of subtribes, as well as a number of poorly understood genera or more limited generic groups. Among the most significant and most interesting of such problems are those noted here:

(1) the infra-generic organization of *Olearia* and its relation to other Australian Hinterhuberinae;
(2) the generic definitions among the taxa comprising the *Chiliotrichum* group within the Hinterhuberinae, especially *Chiliophyllum*, *Chiliotrichopsis*, *Chiliotrichum*, *Diplostephium*, and *Nardophyllum*, where the definitions of generic boundaries currently rely mostly on ray presence or absence, ray color, and various permutations of the pappus;
(3) the internal organization of Old World *Conyza* and the relationship of its groups to New World species;
(4) the origin of *Erigeron*, its internal systematic structure, and its relationship to the other genera placed here in the Conyzinae;
(5) the interrelationships of the major groups within the grangeoid complex;
(6) the infratribal relationships of the western North American, putatively disjunct endemics (e.g., *Aphanostephus*, *Astranthium*, *Rigiopappus*, *Monoptilon*) hypothesized here to be closer to Southern Hemisphere groups than the Northern Hemisphere ones;
(7) the phylogenetic position of *Townsendia*: is it a relictual, basal element of the Brachycominae? Is *T. formosa* an evolutionary fragment more closely related to other Brachycominae than to pappose (typical) *Townsendia*? Do similarities between *Townsendia* and *Amellus* represent relatively distant parallelisms?
(8) the generic definitions among the taxa comprising the *Lagenifera* group within the Lageniferinae;
(9) the internal systematic structure of Old World *Aster* and Asterinae, and their relationship to the Symphyotrichinae;
(10) the nature of the interrelationship between *Galatella* and *Crinitaria*;
(11) the status of the Asian "para-*Brachyactis*," a group of species apparently within the Asterinae and distantly removed from typical *Symphyotrichum* subg. *Brachyactis*.

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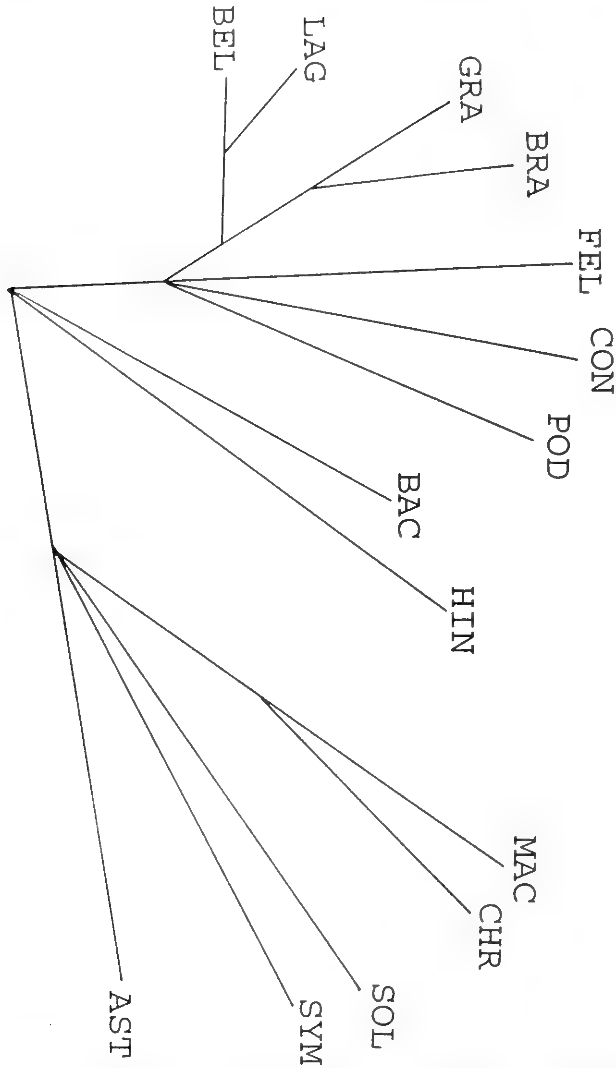

Figure 1. Summary diagram showing subtribes of Astereae, with suggestions regarding phylogeny (see text for comments). Subtribes are abbreviated by their first three letters. The five groups on the right are primarily Northern Hemisphere, the others primarily Southern Hemisphere.

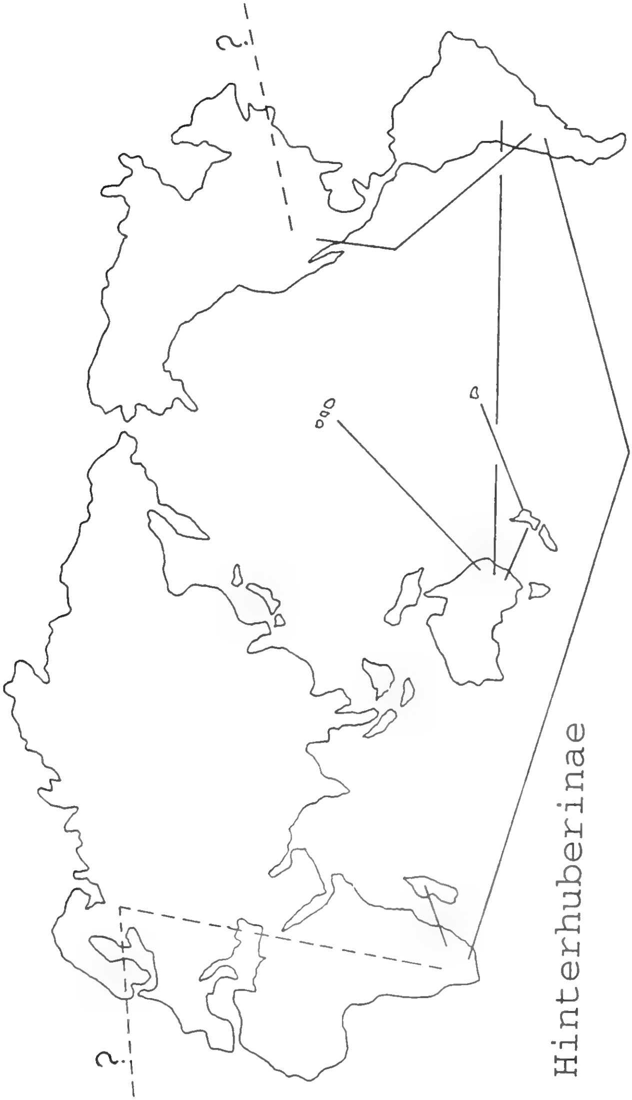

Figure 2. Intercontinental sister-group relationships within the subtribe Hinterhuberinae. An alternative origin for *Ericameria* in western North America is suggested by "?" (see text for comments).

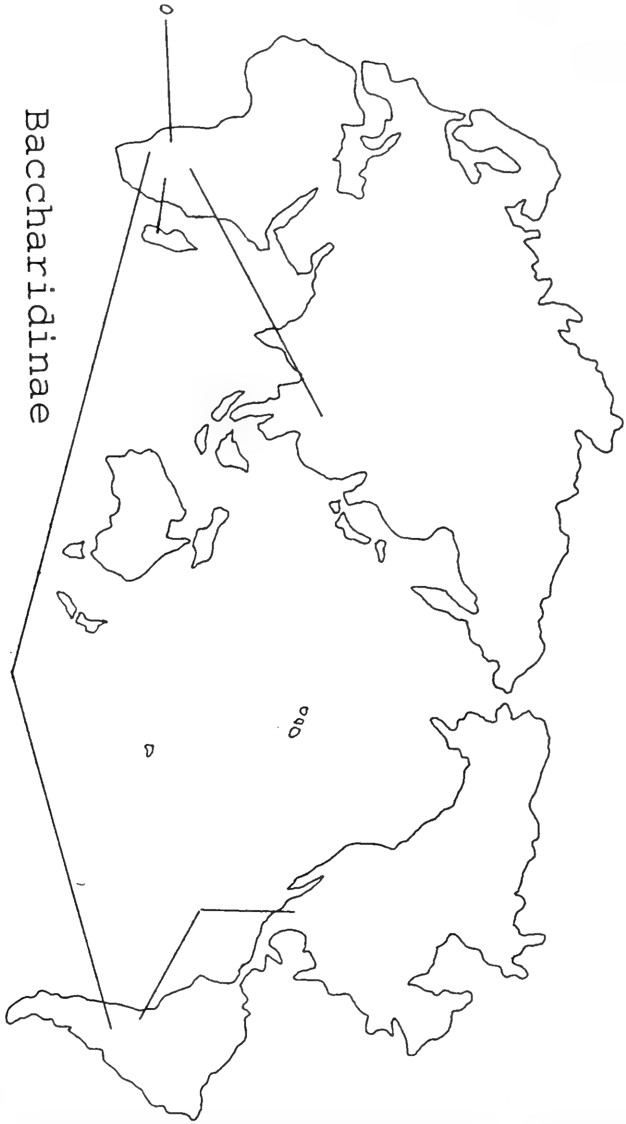

Figure 3. Intercontinental sister-group relationships within the subtribe Baccharidinae.

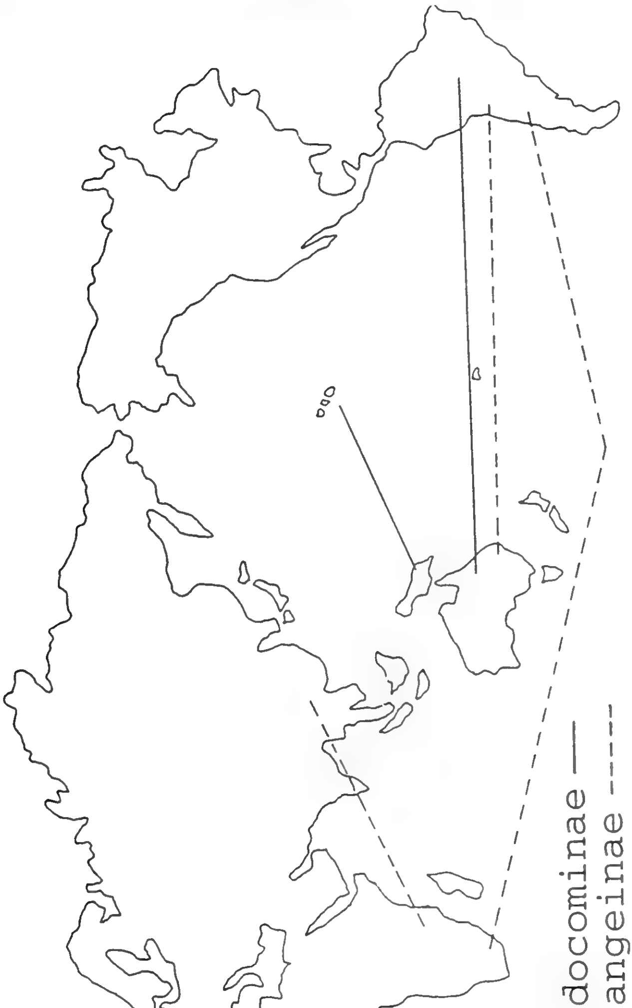

Figure 4. Intercontinental sister-group relationships within the subtribes Podocominae and Grangeinae.

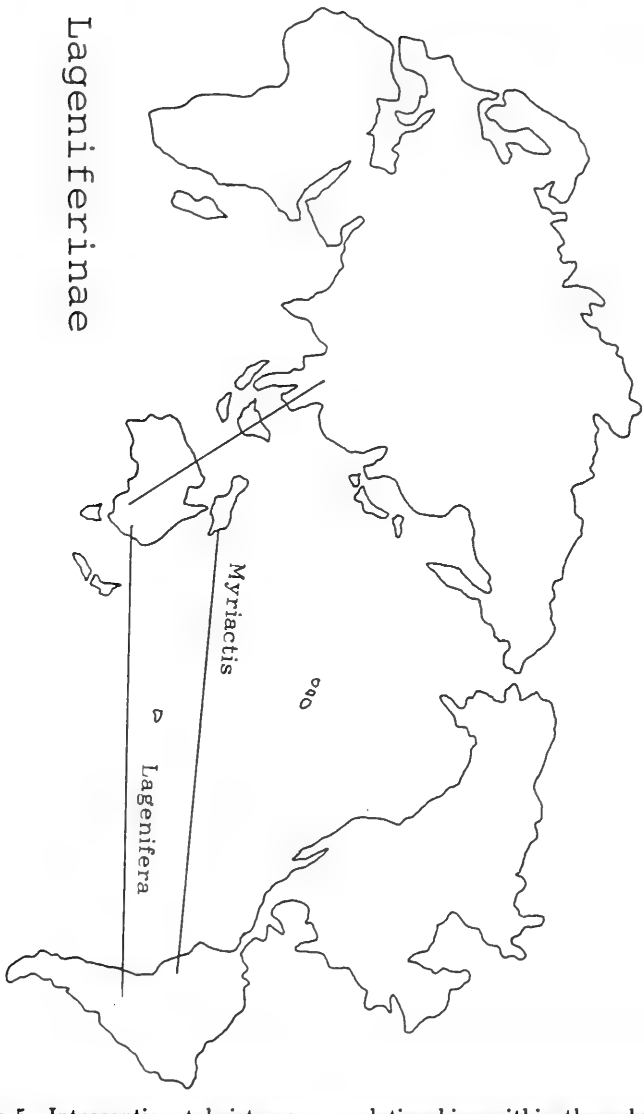

Figure 5. Intercontinental sister-group relationships within the subtribe Lageniferinae.

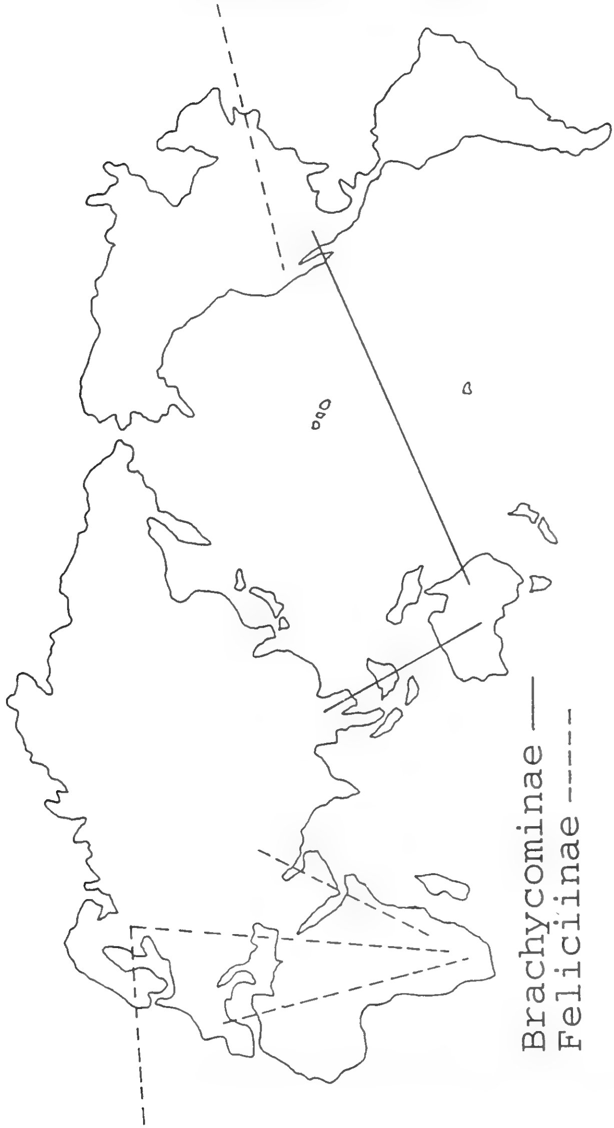

Figure 6. Intercontinental sister-group relationships within the subtribes Brachycominae and Feliciinae.

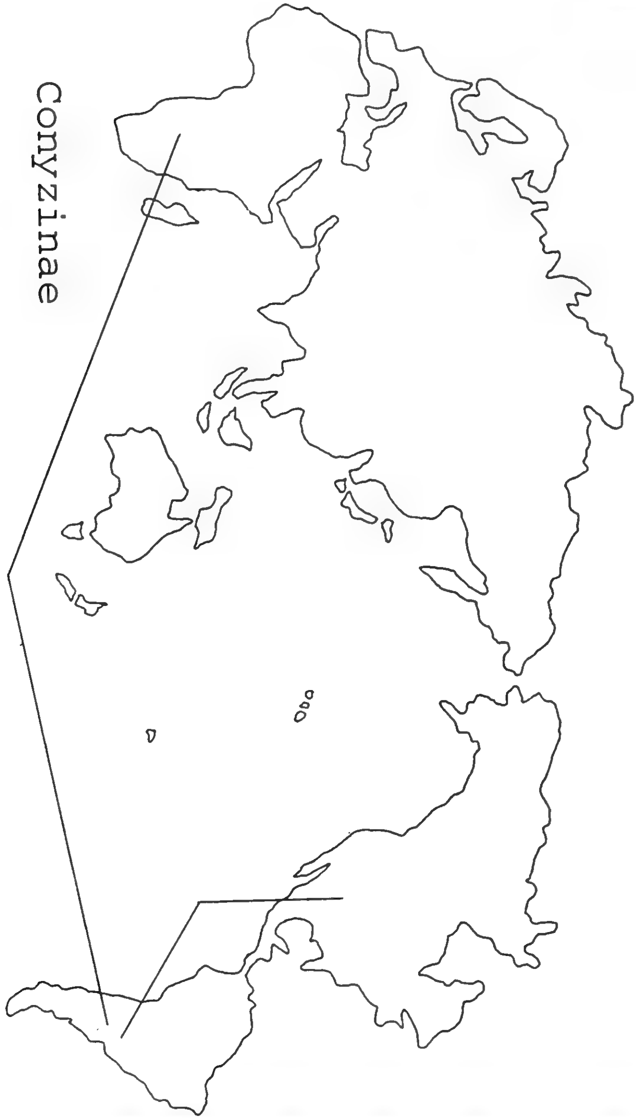

Figure 7. Intercontinental sister-group relationships within the subtribe Conyzinae. The nature of the relationship between African *Conyza* and the New World (typical) element of that genus is not clear (see text for comments).

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LITERATURE CITED

Adams, L.G. 1979. A review of the genus *Solenogyne* (Asteraceae) in Australia and New Zealand. Brunonia 2:43-65.

Anderberg, A.A. 1989. Phylogeny and classification of the tribe Inuleae (Asteraceae). Canad. J. Bot. 67:2277-2296.

________. 1991. Phylogeny and taxonomy of the tribe Gnaphalieae (Asteraceae). Opera Bot. 104:1-195.

________. 1991. Phylogeny and taxonomy of the tribe Plucheae (Asteraceae). Pl. Syst. Evol. 176:145-177.

Anderson, L.C. & P.S. Weberg. 1974. The anatomy and taxonomy of *Vanclevea* (Asteraceae). Great Basin Naturalist 34:151-160.

Bailey, F.M. 1900. *The Queensland Flora.* Part III. Diddams & Co., Brisbane, Australia.

Baker, J.G. 1882. Compositae III. Asteroideae. *In* C.F.P. Martius, *Fl. Bras.* 6(3):1-100.

Barroso, G.M. 1976. Compositae - Subtribo Baccharidinae Hoffmann - Estudo das especies ocorrentes no Brasil. Revista Rodriguesia 40:3-273.

Beaman, J.H. 1957. The systematics and evolution of *Townsendia* (Compositae). Contr. Gray Herb. 183:1-151.

Bentham, G. 1873a. Notes on the classification, history, and geographical distribution of the Compositae. J. Linn. Soc. Bot. 13:335-577.

________. 1873b. Compositae. *In* Bentham, G. & J.D. Hooker. *Gen. Pl.* 2:163-533. A. Black, London, Great Britain.

Black, J.M. 1929. *Flora of South Australia.* Part IV. Bignoniaceae - Compositae. Govt. Printer, Adelaide, South Australia.

Bremer, K. 1993. Intercontinental relationships of African and South American Asteraceae: A cladistic biogeographic analysis. Pp. 105-135 *in* Goldblatt, P., (ed.)., *Biological Relationships Between Africa and South America.* Yale University Press, New Haven, Connecticut.

———. 1994. Asteraceae: cladistics and classification. Timber Press, Portland, Oregon.

Bremer, K., R.K. Jansen, P.O. Karis, M. Kallersjo, S.C. Keeley, K-J. Kim, H.J. Michaels, J.D. Palmer, & R.S. Wallace. 1992. A review of the phylogeny and classification of the Asteraceae. Nord. J. Bot. 12:141-148.

Bremer, K. & C.J. Humphries. 1993. Generic monograph of the Anthemideae (Asteraceae). Bull. Nat. Hist. Mus. London (Bot.) 23(2):71-177.

Brown, G.K. & W.D. Clark. 1982. Taxonomy of *Haplopappus* sect. *Gymnocoma* (Compositae). Syst. Bot. 7:199-213.

Bruhl, J.J. & C.J. Quinn. 1990. Cypsela anatomy in the "Cotuleae" (Asteraceae - Anthemideae). Bot. J. Linn. Soc. 102:37-59.

Burbidge, N.T. 1982. A revision of *Vittadinia* A. Rich. (Compositae) together with a reinstatement of *Eurybiopsis* DC. and a description of a new genus, *Camptacra*. Brunonia 5:1-72.

Cabrera, A.L. 1931. Revisión de las especies sudamericanos del género *Grindelia*. Revista Mus. La Plata 33:207-249.

———. 1966. The genus *Lagenophora* (Compositae). Blumea 14:285-308.

———. 1971. *Flora Patagonica.* Parte VII. Compositae. Colleción Cientifica del INTA, Buenos Aires, Argentina.

Cassini, H.M. 1817. Tableau exprimant les affinites des tribus naturelles de famille des Synantherees. *In* Cuvier, G. (ed.), *Dictionnaire des Sciences Naturelles* 3, ed. 2. Paris, France.

Chen, Y.-l. 1985. An endemic and endangered genus *Heteroplexis* Chang from Guangxi. Guihaia 5(4):337-343.

Clark, W.D. 1979. The taxonomy of *Hazardia* (Compositae: Astereae). Madroño 26:105-127.

Cronquist, A. 1947. Notes on the Compositae of the northeastern United States - V. Astereae. Bull. Torrey Bot. Club 74:142-150.

Cuatrecasas, J. 1969. Prima Flora Columbiana. 3. Compositae-Astereae. Webbia 24:1-335; 25(2):708. 1971.

________. 1977. *Westoniella*, a new genus of the Astereae from the Costa Rican paramos. Phytologia 35:471-487.

________. 1982. Miscellaneous notes on neotropical flora, XV. New taxa in the Astereae. Phytologia 52:166-177.

________. 1986. Un género nuevo de Astereae, Compositae, de Colombia. Anales Jard. Bot. Madrid 42:415-426.

Davis, G.L. 1948. Revision of the genus *Brachycome* Cass. Proc. Linn. Soc. New South Wales 73:142-241.

________. 1950. Revision of the genus *Solenogyne* Cass. Proc. Linn. Soc. New South Wales 75:188-194.

________. 1952. Revision of the genus *Calotis* R. Br. Proc. Linn. Soc. New South Wales 77:146-188.

________. 1964. The embyrology of *Minuria integerrima* (DC.) Benth. Phytomorphology 14:231-329.

DeJong, D.C.D. 1965. A systematic study of the genus *Astranthium* (Compositae, Astereae). Publ. Mus., Michigan State Univ., Biol. Ser. 2(9):433-528.

Dorn, R.D. 1992. *Townsendia microcephala* (Asteraceae: Astereae): a new species from Wyoming. Madroño 39:189-192.

Drury, D.G. 1968. A clarification of the generic limits of *Olearia* and *Pleurophyllum* (Astereae - Compositae). New Zealand J. Bot. 6:459-466.

________. 1974. A broadly based taxonomy of *Lagenifera* sect. *Lagenifera* and *Solenogyne* (Compositae - Astereae) with an account of their species in New Zealand. New Zealand J. Bot. 12:365-395.

Drury, D.G. & L. Watson. 1966. Taxonomic implications of a comparative anatomical study of Inuloideae-Compositae. Amer. J. Bot. 53:828-833.

Dunlop, C.R. 1980a. *Dichromochlamys*, a new genus in Asteraceae (Astereae). J. Adelaide Bot. Gard. 24:235-239.

________. 1980b. A revision of *Ixiochlamys* (Asteraceae: Astereae). J. Adelaide Bot. Gard. 24:241-252.

Elisens, W.J., R.D. Boyd, & A.D. Wolfe. 1992. Genetic and morphological divergence among varieties of *Aphanostephus skirrhobasis* (Asteraceae - Astereae) and related species with different chromosome numbers. Syst. Bot. 17:380-394.

Fayed, A. 1979. Revision der Grangeinae (Asteraceae - Astereae). Mitt. Bot. Staats. München 15:425-576.

Franchet, A. 1896. Compositae novae e flora Sinensi. J. Bot. (Morot) 10:377-386.

Freire, S.E. 1986. *Novenia:* nuevo género de Inuleae (Compositae). Bol. Soc. Argent. Bot. 24:295-304.

Freire, S.E. & F. Hellwig. 1990. A new combination in *Novenia* (Compositae: Inuleae). Taxon 39:124-125.

Given, D.R. 1973. *Damnamenia* gen. nov., a new subantarctic genus allied to *Celmisia* Cass. (Astereae - Compositae). New Zealand J. Bot. 11:785-796.

Graham, A. 1993. History of the vegetation: Cretaceous (Maastrichtian) - Tertiary. Pp. 57-70. *In* Flora of North America Editorial Commit- tee (eds.), *Flora of North America*, Vol. 1. Oxford University Press, New York, New York.

Grau, J. 1970. Die Gattung *Polyarrhena* Cass. (Asteraceae - Astereae). Mitt. Bot. Staats. München 7:347-368.

————. 1971. On the generic delimitation of some South African Astereae. Mitt. Bot. Staats. München 10:275-279.

————. 1973. Revision der Gattung *Felicia* (Asteraceae). Mitt. Bot. Staats. München 4:195-705.

————. 1977. Astereae - systematic review. *In* Heywood, V.H., J.B. Harborne, & B.L. Turner (eds.). *The Biology and Chemistry of the Compositae* 1:539-565. Academic Press, London, Great Britain.

————. 1980. Die Testa der Mutisieae und ihre systematische Bedeutung. Mitt. Bot. Staats. München 16:269-332.

Gray, A. 1880. Contributions to North American botany. I. Notes on some Compositae. Proc. Amer. Acad. Arts 16:78-102.

Grierson, A.J.C. 1964. A revision of the asters of the Himalayan area. Notes Roy. Bot. Gard. Edinb. 26:67-163.

Gupta, R.C. & B.S. Gill. 1989. Cytopalynology of north and central Indian Compositae. J. Cytol. Genet. 24:96-105.

Hall, H.M. 1928. The genus *Haplopappus* - A phylogenetic study in the Compositae. Carnegie Inst. Washington Publ. 389:1-391.

Handel-Mazzeti, H.R.E. 1937. Neue und bemerkenswerte chinesische Compositen, besonders aus dem Berliner Herbar. Notizbl. Bot. Gard. Mus. Berl. Dahl. 13(120):607-661.

Hartman, R.L. 1990. A conspectus of *Machaeranthera* (Asteraceae: Astereae). Phytologia 68:439-465.

Hiern, W.P. 1898. Two new genera of Compositae. J. Bot. Brit. & Foreign 36:289-292.

Hellwig, F.H. 1990. Die Gattung *Baccharis* L. (Compositae - Astereae) in Chile. Mitt. Bot. Staats. München 29:1-456.

________. 1992. Untersuchungen zur Behaarung ausgewahlter Astereae (Compositae). Flora 186:425-444.

________. 1993. The genera *Pingraea* Cassini and *Neomolina* Hellwig (Compositae-Astereae). Candollea 48:203-219.

Heywood, V.H. & C.J. Humphries. 1977. Anthemideae - systematic review. *In* Heywood, V.H., J.B. Harborne, & B.L. Turner (eds.). *The Biology and Chemistry of the Compositae* 2:851-898. Academic Press, London, Great Britain.

Hess, R. 1938. Vergleichende Untersuchungen uber die Zwillingshaare der Compositen. Engler's Bot. Jahrb. 68:435-496.

Hilliard, O.M. & B.L. Burtt. 1973. Notes on some plants of southern Africa chiefly from Natal: III. Notes Royal Bot. Gard. Edinb. 32:303-387.

Hoffmann, O. 1890. Tubuliflorae - Astereae. In *Die Natürlichen Pfanzenfamilien* (A. Engler & K. Prantl [eds.]) 4(5):142-172. Wilhelm Engelmann, Leipzig, Germany.

Huber, W. 1993a. Zur Chemotaxonomie *Erigeron*-Arten (Compositae) der Alpen. Ber. Geobot. Inst. ETH, Zürich 59:124-136.

________. 1993b. Biosystematisch-okologische Untersuchungen an den *Erigeron*-Arten (Asteraceae) der Alpen. Veroffentl. Geobot. Inst. ETH, Zürich 114:1-143.

———— & H. Zhang. 1991. Morphologische und chemotaxonomische untersuchungen an den *Erigeron*-Arten der Alpen. Ber. Geobot. Inst. ETH, Zürich 57:116-164.

———— & A. Leuchtmann. 1992. Genetic differentiation of the *Erigeron* species (Asteraceae) in the Alps: a case of unusual allozymic uniformity. Pl. Syst. Evol. 183:1-16.

Humbert, H. 1960. Flore de Madagascar. Famille 189 - Composees, III. Asterees. 1:204-325.

Jeffrey, C. & Y.-l. Chen. 1984. Taxonomic studies on the tribe Senecioneae (Compositae) of Eastern Asia. Kew Bull. 39:205-446.

Jones, A.G. 1976. Observations on the shape and exposure of style branches in the Astereae (Compositae). Amer. J. Bot. 63:259-262.

Karis, P.O. 1993a. Morphological phylogenetics of the Asteraceae- Asteroideae, with notes on character evolution. Pl. Syst. Evol. 186:69-93.

————. 1993b. Heliantheae sensu lato (Asteraceae), clades and classification. Pl. Syst. Evol. 188:139-195.

Keck, D.D. 1956. *Benitoa*, a new genus of Compositae from California. Leafl. W. Bot. 8:25-28.

Kim, K.-J., R. K. Jansen, R. S. Wallace, H. J. Michaels, & J.D. Palmer. 1992. Phylogenetic implications of rbcL sequence variation in the Asteraceae. Ann. Missouri Bot. Gard. 79:428-445.

Koster, J.T. 1966. The Compositae of New Guinea I. Nova Guinea 24:524-612.

————. 1975. The Compositae of New Guinea IV. Additions and corrections to I, II, and III. Blumea 22:207-217.

Lander, N.S. 1989. *Apostates* (Asteraceae: Astereae), a new genus from the south-eastern Polynesian Island of Rapa. Austr. Syst. Bot. 2:129-133.

Lander, N.S. & R. Barry. 1980a. Reinstatement of the genus *Kippistia* F. Muell. (Asteraceae - Astereae). Nuytsia 3:215-219.

——————————. 1980b. A review of the genus *Minuria* DC. (Asteraceae - Astereae). Nuytsia 3:221-237.

Lane, M.A. 1993a. New combinations in Californian *Lessingia* (Compositae: Astereae). Novon 3:213-214.

________. 1993b. *Lessingia*. Pp. 304-306 *in* Hickman, J.C. (ed.), *The Jepson Manual, Higher Plants of California*. Univ. California Press, Berkeley, California.

________ & J. Li. 1993. Documented chromosome numbers 1993:1. Chromosome number reports in Compositae with emphasis on tribe Astereae of the southwestern United States and Mexico. Sida 15:539-546.

________ & R.K. Jansen. 1990. Chloroplast DNA restriction site evidence for relationships of genera of Astereae (Compositae). Amer. J. Bot. 77(6:2, abstract):143.

Lavin, M. & M. Luckow. 1993. Origins and relationships of tropical North America in the context of the boreotropics hypothesis. Amer. J. Bot. 80:1-14.

Ling, Y. & Y.-l. Chen. 1965. Genera nova vel minus cognita familiae Compositarum, II. *Cavea* W.W. Smith et Small et *Nannoglottis* Maxim. Acta Phytotax. Sin. 10:91-102.

Ling, Y., Y.-l. Chen, & Z. Shi. 1985. Astereae. *Flora Reipublicae Popularis Sinicae*, Compositae (1). Tomus 74:73-353. Academia Sci. Sinica, Peiping, China.

Lowrey, T.K. 1986. A biosystematic revision of Hawaiian *Tetramolopium* (Compositae - Astereae). Allertonia 4:204-264.

Macloskie, G. 1883. The achenial hairs of *Townsendia*. Amer. Nat. 17:1102-1107.

Moore, S.M. 1875. Description of some new phanerogamia collected by Dr. Shearer, at Kiukiang, China. J. Bot. Brit. Foreign 13:225-231.

Morgan, D.R. 1990. A systematic study of *Machaeranthera* (Asteraceae) and related groups using restriction analysis of chloroplast DNA and a taxonomic revision of *Machaeranthera* section *Psilactis*. Ph.D. dissertation, Univ. Texas, Austin, Texas.

________ & B.B. Simpson. 1992. A systematic study of *Machaeranthera* (Asteraceae) and related groups using restriction site analysis of chloroplast DNA. Syst. Bot. 17:511-531.

Nesom, G.L. 1976. A new species of *Erigeron* (Asteraceae) and its relatives in southwestern Utah. Brittonia 28:263-272.

________. 1989a. The separation of *Trimorpha* (Compositae: Astereae) from *Erigeron*. Phytologia 67:61-66.

———. 1989b. Infrageneric taxonomy of New World *Erigeron* (Compositae: Astereae). Phytologia 67:67-93.

———. 1989c. Taxonomy of *Erigeron* sect. *Polyactis* (Compositae: Astereae). Phytologia 66:415-455.

———. 1990a. Taxonomy of the genus *Laennecia* (Asteraceae: Astereae). Phytologia 68:205-228.

———. 1990b. Further definition of *Conyza* (Asteraceae: Astereae). Phytologia 68:229-233.

———. 1990c. Taxonomy of the *Erigeron coronarius* group of *Erigeron* sect. *Geniculactis* (Asteraceae: Astereae). Phytologia 69:237-253.

———. 1991a. Union of *Bradburia* with *Chrysopsis* (Asteraceae: Astereae), with a phylogenetic hypothesis for *Chrysopsis*. Phytologia 71:109-121.

———. 1991b. A phylogenetic hypothesis for the goldenasters (Asteraceae: Astereae). Phytologia 71:136-151.

———. 1991c. Redefinition of *Hesperodoria* (Asteraceae: Astereae) and the segregation of *Columbiadoria*, a new monotypic genus from western North America. Phytologia 71:244-251.

———. 1991d. Transfer of *Aster kingii* (Asteraceae: Astereae) to *Tonestus*. Phytologia 71:122-127.

———. 1992a. *Oritrophium orizabense* (Asteraceae: Astereae), a new species and the first report of the genus from North and Central America. Phytologia 73:338-344.

———. 1992b. Transfer of *Chaetopappa elegans* to *Ionactis* (Asteraceae: Astereae). Phytologia 73:416-424.

———. 1992c. Revision of *Erigeron* sect. *Linearifolii* (Asteraceae: Astereae). Phytologia 72:157-208.

———. 1992d. Taxonomic notes on *Erigeron* (Asteraceae: Astereae) of California, Nevada, and Arizona. Phytologia 73:186-202.

———. 1993a. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and comments on their phylogenetic position. Phytologia 75:1-44.

———. 1993b. *Aztecaster* (Asteraceae: Astereae), a new ditypic genus of dioecious shrubs from México with redefinitions of the subtribes Hinterhuberinae and Baccharidinae. Phytologia 75:55-73.

_______. 1993c. *Madagaster* (Asteraceae: Astereae), a new genus of subtribe Hinterhuberinae. Phytologia 75:94-99.

_______. 1993d. A Cuban endemic: *Hysterionica marginata* (Asteraceae: Astereae) rather than *Aster grisebachii*. Phytologia 75:163-165.

_______. 1993e. Taxonomic status of *Nardophyllum scoparium* (Asteraceae: Astereae), with observations on the limits of *Nardophyllum*. Phytologia 75:358-365.

_______. 1993f. Synopsis of *Parastrephia* (Asteraceae: Astereae). Phytologia 75:347-357.

_______. 1993g. First report of *Floscaldasia* (Asteraceae: Astereae) in Ecuador and comments on its relationships. Phytologia 75:366-368.

_______. 1993h. Taxonomy of *Doellingeria* (Asteraceae: Astereae). Phytologia 75:452-462.

_______. 1994a. Reinstatement of the South American genus *Leptostelma* (Asteraceae: Astereae). Phytologia, in press.

_______. 1994b. *Apopyros* (Asteraceae: Astereae), a new genus from southern Brazil, Argentina, and Paraguay. Phytologia 76:176-184.

_______. 1994c. Separation of *Neja* (Asteraceae: Astereae) from *Hysterionica*. Phytologia 76:168-175.

_______. 1994d. *Inulopsis* synopsis (Asteraceae: Astereae). Phytologia 76:115-124.

_______. 1994e. Comments on *Microgynella*, *Sommerfeltia*, and *Asteropsis* (Asteraceae: Astereae). Phytologia 76:101-105.

_______. 1994f. *Peripleura* (Asteraceae: Astereae): a new, Australian genus segregated from *Vittadinia*. Phytologia 76:125-135.

_______. 1994g. Taxonomic dispersal of Australian *Erigeron* (Asteraceae: Astereae). Phytologia 76:143-159.

_______. 1994h. *Pytinicarpa* (Asteraceae: Astereae), a new genus from New Caledonia. Phytologia 76:136-142.

_______. 1994i. Repartition of *Mairia* (Asteraceae: Astereae). Phytologia 76:85-95.

_______. 1994j. *Pacifigeron* (Asteraceae: Astereae), a new genus from the Polynesian island of Rapa. Phytologia 76:160-167.

———. 1994k. Review of the taxonomy of *Aster* sensu lato (Asteraceae: Astereae). Phytologia in press.

———. 1994l. *Erigeron pattersonii* (Asteraceae: Astereae), a new species from Nuevo León, México. Phytologia 76:96-100.

——— & D.R. Morgan. 1990. Reinstatement of *Tonestus* (Asteraceae: Astereae). Phytologia 68:174-180.

———, D.R. Morgan, Y. Suh, & B.B. Simpson. 1990. *Xylothamia* (Asteraceae: Astereae), a new genus related to *Euthamia*. Sida 14:101-116.

——— & T.J. Leary. 1992. A new species of *Ionactis* (Asteraceae: Astereae) and an overview of the genus. Brittonia 44:247-252.

——— & G.I. Baird. 1993. Completion of *Ericameria* (Asteraceae: Astereae), diminution of *Chrysothamnus*. Phytologia 75:74-93.

———, Y. Suh, & B.B. Simpson. 1993. *Prionopsis* (Asteraceae: Astereae) united with *Grindelia*. Phytologia 75:341-346.

——— & D. Zanowiak. 1994. Taxonomic overview of *Podocoma* (Astereae: Asteraceae), with the incorporation of two species from *Conyza*. Phytologia 76:106-114.

Nishikawa, T. 1985. Chromosome counts of flowering plants of Hokkaido (9). J. Hokkaido Univ. Educ., Sect. 2B 36:25-40.

Ornduff, R. & B.A. Bohm. 1975. Relationships of *Tracyina* and *Rigiopappus*. Madroño 23:53-55.

Ralston, B.G., G. Nesom, & B.L. Turner. 1989. Documented plant chromosome numbers 1989:1. Chromosome numbers in Mexican Asteraceae with special reference to the tribe Tageteae. Sida 13:359-368.

Ramayya, N. 1962. Studies on the trichomes of some Compositae II. Phylogeny and classification. Bull. Bot. Surv. India 4:189-192.

Raven, P.H. 1971. The relationship between 'mediterranean' floras. Pp. 119-134, *in* P.H. Davis, P.C. Harper, & I.C. Hedge (eds.), "Plant Life of Southwest Asia." Bot. Soc. Edinburgh.

——— & D.I. Axelrod. 1974. Angiosperm biogeography and past continental movement. Ann. Missouri Bot. Gard. 61:539-673.

Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithson. Contr. Bot. 51:1-102.

Robinson, H. & R.D. Brettell. 1972. Tribal revisions in the Asteraceae. I. The relationship of *Geissolepis*. Phytologia 24:299-301.

__________________. 1973a. Tribal revisions in the Asteraceae. VII. The relationship of *Isoetopsis*. Phytologia 26:73-75.

__________________. 1973b. Tribal revisions in the Asteraceae. V. The relationship of *Rigiopappus*. Phytologia 26:69-70.

__________________. 1973c. Tribal revisions in the Asteraceae. X. The relationship of *Plagiocheilus*. Phytologia 26:159-162.

Rommel, A. 1977. Die Gattung *Amellus* L. (Asteraceae - Astereae), Systematischer Teil. Mitt. Bot. Staats. München 13:579-728.

Ryding, O. & K. Bremer. 1992. Phylogeny, distribution, and classification of the Coreopsideae (Asteraceae). Syst. Bot. 17:649-659.

Skvarla, J.J., B.L. Turner, V.C. Patel, & A.S. Tomb. 1977. Pollen morphology in the Compositae and in morphologically related families. *In* Heywood, V.H., J.B. Harborne, & B.L. Turner (eds.). *The Biology and Chemistry of the Compositae* 1:141-265. Academic Press, London, Great Britain.

Scott, A.J. 1990. Notes on Compositae-Astereae for the 'Flore des Mascareignes.' Kew Bull. 46:339-353.

Semple, J.C., V.C. Blok, & P. Heiman. 1980. Morphological, anatomical, habit, and habitat differences among the goldenaster genera *Chrysopsis*, *Heterotheca*, and *Pityopsis* (Compositae-Astereae). Canad. J. Bot. 58:147-163.

Shinners, L.H. 1949. Revision of the genus *Egletes* Cassini north of South America. Lloydia 12:239-250.

Smith, W. & J. Small. 1922. *Formania*: a new genus of the Compositae from Yunnan. Trans. Proc. Bot. Soc. Edinb. 28:91-92.

Soreng, R.J. & R.W. Spellenberg. 1984. An unusual new *Chaetopappa* (Asteraceae - Astereae) from New Mexico. Syst. Bot. 9:1-5.

Sorensen, N.A. 1977. Polyacetylenes and conservatism of chemical characters in the Compositae. *In* Heywood, V.H., J.B. Harborne, & B.L. Turner (eds.). *The Biology and Chemistry of the Compositae* 1:385-409. Academic Press, London, Great Britain.

Spongberg, S.A. 1971. A systematic and evolutionary study of North American arctic and alpine monocephalous species of *Erigeron* (Compositae). Ph.D. dissertation, University of North Carolina, Chapel Hill, North Carolina.

Stace, C.A. (ed.). 1975. *Hybridization and the Flora of the British Isles.* Academic Press, London, Great Britain.

Suh, Y. 1989. Phylogenetic studies of North American Astereae (Asteraceae) based on chloroplast DNA. Ph.D. dissertation, Univ. Texas, Austin, Texas.

Taylor, D.W. 1988a. Paleobiogeographic relationships of the Paleogene flora from the southeastern U.S.A.: implications for West Gondwanaland affinities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 66:265-275.

———. 1988b. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. Bot. Rev. 56:279-417.

Tiffney, B.H. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arnold Arb. 66:73-94.

———. 1985b. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J. Arnold Arb. 66:243-273.

Turner, B.L. 1970. Chromosome numbers in the Compositae XII. Australian species. Amer. J. Bot. 5:382-389.

———. 1977. Fossil history and geography. *In* Heywood, V.H., J.B. Harborne, & B.L. Turner (eds.). *The Biology and Chemistry of the Compositae* 1:21-39. Academic Press, London, Great Britain.

———. 1984. Taxonomy of the genus *Aphanostephus* (Asteraceae - Astereae). Phytologia 56:81-101

Van Horn, G.S. 1973. The taxonomic status of *Pentachaeta* and *Chaetopappa* with a revision of *Pentachaeta.* Univ. Calif. Publ. Bot. 65:1-41.

Velez, M.C. 1981. Carpologische Untersuchungen an amerikanischen Astereae (Compositae). Mitt. Bot. Staats. München 17:1-170.

Wagner, W.L. & D.R. Herbst. 1987. A new species of *Remya* (Asteraceae - Astereae) on Kauai and a review of the genus. Syst. Bot. 12:601-608.

Welsh, S.L. & J.L. Reveal. 1968. A new species of *Townsendia* (Compositae) from Utah. Brittonia 20:375-377.

Wild, H. 1969a. The genus *Nidorella* Cass. Bol. Soc. Brot. 43:209-243.

________. 1969b. The species of *Conyza* with ligulate or lobed ray florets in Africa, Madagascar and the Cape Verde Islands. Bol. Soc. Brot. 43:243-272.

Wolfe, J.A. 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. Ann. Missouri Bot. Garden 62:264-279.

Zanowiak, D.J. 1991. An analysis of systematic and phyletic relationships within Baccharidinae (Asteraceae: Astereae). Ph.D. dissertation, Texas A & M Univ., College Station, Texas.

Zardini, E.M. 1985. Revisión del género *Noticastrum* (Compositae - Astereae). Revista Mus. La Plata, Secc. Bot. 13:313-424.

Zhang, X. & K. Bremer. 1993. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. Pl. Syst. Evol. 184:259-283.

APPENDIX I. GENERA OF ASTEREAE

For ease of reference, the genera of Astereae in the evaluation presented here are listed below by major geographical area with authorities and number of species. If a genus occurs in more than one area, it is listed under the area of its primary center of diversity and abundance. Only recent or relatively controversial generic synonyms (SYN=) are provided. Subtribes are indicated by the first three letters of the subtribe (all capitals) at the end of the generic entry.

NORTH AND CENTRAL AMERICA (70 genera)

Acamptopappus A. Gray (2) SOL
Almutaster A. & D. Löve (1) SYM
Amphiachyris (DC.) Nutt. (2) SOL
Amphipappus Torr. & Gray (1) SOL
Aphanostephus DC. (4) BRA
Archibaccharis Heering (32) BAC
Astranthium Nutt. (11) BRA
Aztecaster Nesom (2) HIN
Benitoa Keck (1) MAC
Bigelowia DC. (2) SOL
Boltonia L'Herit. (5) AST
Chaetopappa DC. (11) FEL
SYN= *Leucelene* E. Greene
Chloracantha Nesom, Suh, Morgan, Sundberg, & Simpson (1) SYM
Chrysoma Nutt. (1) SOL

Chrysopsis (Nutt.) Ell. (10) CHR
SYN= *Bradburia* Torr. & Gray
Chrysothamnus Nutt. (14) SOL
SYN= *Hesperodoria* E. Greene
SYN= *Petradoria* E. Greene
Columbiadoria Nesom (1) SOL
Corethrogyne DC. (ca. 1) MAC
Croptilon Rafin. (3) CHR
Dichaetophora A. Gray (1) BRA
Doellingeria Nees (15) SYM
Eastwoodia Brandegee (1) SOL
Ericameria Nutt. (31) HIN
SYN= *Asiris* Nutt.
SYN= *Macronema* Nutt.
SYN= *Stenotopsis* Rydb.
Erigeron L. (ca. 413) CON
SYN= *Achaetogeron* A. Gray
SYN= *Darwiniothamnus* Harling
SYN= *Trimorpha* Cass.
SYN= *Wyomingia* A. Nels.
Eucephalus Nutt. (11) SYM
Euthamia Nutt. (6) SOL
Geissolepis B. Rob. (1) BRA
Grindelia Willd. (ca. 75) MAC
SYN= *Prionopsis* Nutt.
Gundlachia A. Gray (9) SOL
Gutierrezia Lag. (26) SOL
SYN= *Greenella* A. Gray
Gymnosperma Less. (1) SOL
Hazardia E. Greene (13) MAC
Heleastrum DC. (25) SYM
SYN= *Biota* DC.
SYN= *Weberaster* Löve & Löve
Herrickia Woot. & Standl. (5) SYM
Heterotheca Cass. (ca. 25) CHR
Ionactis E. Greene (5) AST
Isocoma Nutt. (16) MAC
Laennecia Cass. (15) POD
Lessingia Cham. (12) MAC
Machaeranthera Nees (30) MAC
SYN= *Eriocarpum* Nutt.
SYN= *Leucosyris* E. Greene
SYN= *Sideranthus* Nutt. *ex* Nees
Monoptilon Torr. & Gray (2) FEL
SYN= *Eremiastrum* A. Gray
Oclemena E. Greene (3) SYM
Oligoneuron Small (6) SOL
SYN= *Unamia* E. Greene
Olivaea Sch.-Bip. *ex* Benth. (2) MAC
Oonopsis E. Greene (3) MAC
Oreochrysum Rydb. (1) SOL
Oreostemma E. Greene (3) SYM
Osbertia E. Greene (3) CHR
Pentachaeta Nutt. (6) FEL
"phyllocephalus group" (3) MAC
Pityopsis Nutt. (8) CHR
Psilactis A. Gray (6) SYM
Pyrrocoma W. Hook. (ca. 12) MAC
Rigiopappus A. Gray (1) FEL
Sericocarpus Nees (5) SYM
Solidago L. (ca. 100) SOL
SYN= *Brachychaeta* Torr. & Gray
SYN= *Brintonia* E. Greene
Stenotus Nutt. (6) SOL
Stephanodoria E. Greene (1) MAC
Symphyotrichum Nees (96) SYM
SYN= *Brachyactis* Ledeb.
SYN= *Conyzanthus* Tamamsch.
SYN= *Mesoligus* Rafin.
SYN= *Virgulus* Rafin.
Tonestus A. Nels. (7) SYM
Thurovia Rose (1) SOL
Tomentaurum Nesom (1) CHR
Townsendia W. Hook. (24) BRA
Tracyina S.F. Blake (1) FEL
Vanclevea E. Greene (1) SOL
Westoniella Cuatr. (6) HIN
Xanthisma DC. (1) MAC
Xanthocephalum Willd. (6) MAC
Xylorhiza Nutt. (8) MAC
Xylothamia Nesom, Morgan, Suh, & Simpson (9) SOL

SOUTH AMERICA (31 genera)
Apopyros Nesom (2) CON
Asteropsis Less. (1) POD

Baccharis L. (ca. 350) BAC
SYN= *Baccharidastrum* Cabrera
SYN= *Baccharidopsis* Barroso
SYN= *Neomolina* Hellwig
SYN= *Pingraea* Cass.
SYN= *Pseudobaccharis* Cabrera
Blakiella Cuatr. (1) HIN
Chiliophyllum Phil. (3) HIN
Chiliotrichum Cass. (2) HIN
Chiliotrichopsis Cabrera (3) HIN
Conyza L. (ca. 80) CON
Diplostephium Kunth (ca. 90) HIN
Egletes Cass. (10) GRA
Floscaldasia Cuatr. (1) HIN
Flosmutisia Cuatr. (1) HIN
Haplopappus DC. (ca. 70) MAC
Heterothalamus Less. (8) BAC
Hinterhubera Sch.-Bip. (8) HIN
Hysterionica Willd. (7) CON
Inulopsis O. Hoffm. (4) POD
Laestadia Kunth (6) HIN
Lepidophyllum Cass. (1) HIN
Leptostelma D. Don (5) CON
Llerasia Triana (14) HIN
Microgynella Grau (1) POD
Nardophyllum Hook. & Arn. (9) HIN
SYN= *Aylacophora* Cabrera
SYN= *Palaeapappus* Cabrera
Neja D. Don (6) CON
Noticastrum DC. (20) CHR
Novenia Freire (1) HIN
Oritrophium (Kunth) Cuatr. (ca. 15) HIN
Parastrephia Nutt. (3) HIN
Plagiocheilus Arn. *ex* DC. (7) GRA
Podocoma Cass. (8) POD
Sommerfeltia Less. (1) POD

EUROPE AND ASIA (22 genera)
Arctogeron DC. (1) AST
Aster L. (ca. 180) AST
SYN= *Bellidiastrum* Cass.
SYN= *Chlamydites* Drumm.
SYN= *Wardaster* J. Small
SYN= *Turczaninowia* DC.
Asterothamnus Novop. (7) AST
Bellis L. (8) AST
Bellium L. (4) BEL
Callistephus C.A. Mey. (1) AST
Chamaegeron Schrenk. (4) HOM
Crinitaria Cass. (13) AST
SYN= *Linosyris* Cass. 1825, *non* Ludw. 1757
SYN= *Pseudolinosyris* Novopokr.
Cyathocline Cass. (3) GRA
Galatella DC. (ca. 30) AST
Heteropappus Less. (20) AST
Heteroplexis C.C. Chang (3) BAC
Kalimeris Cass. (8) AST
SYN= *Asteromoea* Blume
Kemulariella Tamamsch. (6) AST
Krylovia Schischk. (4) AST
Lachnophyllum Bunge (2) HOM
Miyamayomena Kitam. (5) AST
SYN= *Gymnaster* Kitam.
Nannoglottis Maxim. (9) SOL
"para-*Brachyactis*" (ca. 5) AST
Psychrogeton Boiss. (20) AST
Sheareria S. Moore (2) LAG
Tripolium Nees (1) AST

AUSTRALIA AND SOUTHWEST PACIFIC ISLANDS (35 genera)
Achnophora F. Mueller (1) HIN
Brachycome Cass. (ca. 75) BRA
Calotis R. Br. (26) BRA
SYN= *Tolbonia* O. Kuntze
Camptacra N. Burbidge (2) POD
Celmisia Cass. (ca. 60) HIN
Centipeda Lour. (6) GRA
Ceratogyne Turcz. (1) BRA
Damnamenia Given (1) HIN
Dichromochlamys Dunlop (1) POD
Dimorphocoma F. Mueller & R. Tate (1) POD

Elachanthus F. Mueller (2) POD
Erodiophyllum F. Mueller (2) GRA
Iotasperma Nesom (2) POD
Ixiochlamys F. Mueller & Sonder *ex* Sonder (4) POD
Keysseria Lauerb. (9) LAG
Kippistia F. Mueller (1) POD
Lagenifera Cass. (14) LAG
SYN= *Microcalia* A. Rich.
Lagenithrix Nesom (2) LAG
Lagenopappus Nesom (ca. 5) LAG
Minuria DC. (10) POD
SYN= *Eurybiopsis* DC.
Myriactis Less. (12) LAG
Olearia Moench (ca. 100) HIN
Pachystegia Cheeseman (1) HIN
Pacifigeron Nesom (1) HIN
Peripleura (Burbidge) Nesom (9) POD
Piora Koster (1) LAG
Pleurophyllum J.D. Hook. (3) HIN
Pytinicarpa Nesom (2) LAG
Remya W. Hillebr. *ex* Benth. (3) HIN
Rhamphogyne S. Moore (2) LAG
Rhynchospermum Reinw. (1) LAG
Solenogyne Cass. (3) LAG
Tetramolopium Nees (37) POD
Thespis DC. (3) LAG
Vittadinia A. Rich. (20) POD

AFRICA-MADAGASCAR-SOUTH ATLANTIC (31 genera)
Amellus L. (12) HOM
Ceruana Forssk. (1) GRA
Chrysocoma L. (20) HOM
Colobanthera Humbert (1) GRA
Commidendron Berch. *ex* DC. (4) BAC
Dacryotrichia H. Wild (1) GRA
Dichrocephala L'Herit. (10) GRA
Engleria O. Hoffm. (2) HOM
Felicia Cass. (85) HOM
Grangea Adanson (10) GRA
SYN= *Microtrichia* DC.
Grangeopsis Humbert (1) GRA
Grauanthus Fayed (2) GRA
Gymnostephium Less. (8) HOM
Gyrodoma H. Wild (1) GRA
Heteromma Benth. (3) GRA
Jeffreya H. Wild (1) HOM
Madagaster Nesom (5) HIN
Mairia Nees (3) HIN
Melanodendron DC. (1) BAC
Microglossa DC. (ca. 18) BAC
Nidorella Cass. (ca. 15) GRA
Nolletia Cass. (10) HOM
Poecilolepis Grau (2) HOM
Polyarrhena Cass. (4) HOM
Psiadia N.J. Jacquin (ca. 60) BAC
Psiadiella Humbert (1) BAC
Pteronia L. (ca. 80) HIN
Rochonia DC. (4) HIN
Sarcanthemum Cass. (1) BAC
Vernoniopsis Humbert (1) BAC
Zyrphelis Cass. (10) HOM

BOOKS RECEIVED

Flora Europaea: Volume 1: Psilotaceae to Platanaceae. Second Edition. T.G. Tutin†, N.A. Burges, A.O. Chater, J.R. Edmondson, V.H. Heywood, D.M. Moore, D.H. Valentine†, S.M. Walters, & D.A. Webb (eds.). Cambridge University Press, 40 West 20th Street, New York, New York 10011-4211. xlvi. 581 pp. $200.00, ISBN 0-521-41007-x (hardcover).

This second edition contains updated treatments for the included families in the European flora. Designed essentially as in the previous edition, keys to families are lacking, although once a family is determined, the generic and species keys appear to be workable. Appendices including abbreviations for authors and publications are included and useful. The glossary is very brief. Maps at the end of the text codify geographic areas referred to in the text (*i.e.*, western Europe). This and the remaining volumes in the series will undoubtedly be the standard flora for workers on the European continent for some time to come.

Snakes, Ecology & Behavior. Richard A. Seigel & Joseph T. Collins (eds.). McGraw-Hill, Inc., 11 West 19th Street, New York, New York 10011. xvi. 414 pp. $27.95, ISBN 0-07-056056-0 (paper).

Billed as "the most comprehensive survey of snake biology available in a single volume" (from cover), this book is a compilation of treatises by sixteen authors on various aspects of snake ecology and behavior. Although "descended" in a sense from a 1987 volume entitles *Snakes: Ecology and Evolutionary Biology*, very little overlap exists between the two volumes in terms of the authors and subjects treated by any given author. Topics range from discussions of snake niches and habitats (arboreal snakes, foraging theory, habitat selection, thermal ecology), to snake reproduction (sexual dimorphism, mating systems, population genetics), to snake perceptual mechanisms, and snake conservation. The book wraps up with a summary of future research on snakes.

Information for Authors

Articles from botanical systematics and ecology, including biographical sketches, critical reviews, and summaries of literature will be considered for publication in PHYTOLOGIA. Manuscripts may be submitted either on computer diskette, or as typescript. Diskettes will be returned to authors after action has been taken on the manuscript. Diskettes may be 5.25 inches or 3.5 inches and may be written in any IBM or MacIntosh compatible format. Typescript manuscripts should be single spaced and will be read into the computer using a page scanner. The scanner will read standard typewriter fonts but will not read dot matrix print. Manuscripts submitted in dot matrix print cannot be accepted. Use underscore (not italics) for scientific names. Corrections made on typescript manuscripts must be complete and neat as the scanner will not read them otherwise. Language of manuscripts may be either English or Spanish. Figures will be reduced to fit within limits of text pages and therefore, should be submitted with an internal scale and have dimensions proportional to those for text pages. Legends for figures should be included in figures whenever possible. Each manuscript should have an abstract and key word list. Specimen citations should be consistent throughout the manuscript. Serial titles should be cited with abbreviations used in *Botanico Periodicum Huntianum*. References cited only as part of nomenclatural summaries should not appear in Literature Cited. Nomenclatural work should include one paragraph per basionym and must provide proper (as defined by the current *International Code of Botanical Nomenclature)* citation of sources of epithets and combinations.

Authors should arrange for two workers in the appropriate field to review the manuscript before submission. Copies of reviews should be forwarded to the editor with the manuscript. Manuscripts will not be published without review.

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